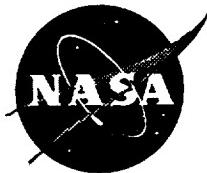




Seed-to-Seed Growth of Superdwarf Wheat and *Arabidopsis* Using Red Light-Emitting Diodes (LEDs): A Report on Baseline Tests Conducted for NASA's Proposed Plant Research Unit (PRU)

G. D. Goins, N. C. Yorio, M. M. Sanwo, and C. S. Brown



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ABSTRACT

Red light-emitting diodes (LEDs) are a potential light source for growing plants in space flight systems because of their superior safety and reliability, small mass and volume, wavelength specificity, electrical efficiency, and longevity. To determine the influence of narrow-spectrum red LEDs on plant growth and seed production, wheat [*Triticum aestivum* L. cv. Superdwarf] and *Arabidopsis* (*Arabidopsis thaliana* (L.) Heynh, race Columbia) plants were grown under red LEDs (peak emission 660 nm) and compared to plants grown under daylight fluorescent (white) light and red LEDs supplemented with either 1% or 10% blue fluorescent (BF) light. Except for longer flag leaves, wheat growth under red LEDs alone appeared normal (i.e. similar to the white light controls), whereas *Arabidopsis* grown under red LEDs alone developed curled leaf margins and a spiraling growth pattern. Wheat and *Arabidopsis* at 15 and 20 days after planting (DAP) respectively, exhibited significantly lower total fresh and dry weight when grown under red LEDs with or without 1% BF light than did plants grown under red LEDs + 10% BF light or plants grown under white light. Between 40 DAP and senescence, wheat had longer flag leaves, and *Arabidopsis* partitioned significantly more dry weight in vegetative tissue when grown under red LEDs alone compared to plants grown under all other light treatments. Wheat showed a slight delay in seed development under all the red LED treatments relative to the control wheat under white light. *Arabidopsis* grown under red LEDs alone required 60-70 days to set seed, however, *Arabidopsis* under all other light regimes successfully set seed within 40 DAP. Both wheat and *Arabidopsis* under red LEDs alone, or red LEDs + 1% BF light, had a significantly lower seed yield than did plants grown under white light. The addition of 10% BF light to red LEDs, however, partially alleviated the adverse effect of red LEDs on yield. Irrespective of the light treatment, viable seeds were produced by wheat (75-92% germination rate) and *Arabidopsis* (85-100% germination rate). These results indicate that wheat, and to a lesser extent *Arabidopsis*, can be grown successfully under red LEDs alone, but supplemental blue light is required with red LEDs to match the growth characteristics and seed yield associated with plants grown under white light.

INTRODUCTION

Light is the energy source for photosynthesis, and it regulates many aspects of plant development. A major challenge to growing plants in space is controlling and supplying sufficient quantity and quality of light (Langhans and Dreesen, 1988; Sager and Wheeler, 1992). Light-emitting diodes (LEDs) are a promising electric light source for space-based plant growth systems because of the LEDs' small mass and volume, solid state construction, electrical efficiency, superior safety, and operational longevity (Barta et al., 1992; Bula et al., 1991). Red LEDs emit a narrow spectrum of light (660 nm with 25 nm bandwidth at half peak height) corresponding to the maximum absorbance of chlorophyll. Although red LEDs have great potential for use as a light source to drive photosynthesis, plants are adapted to utilize a wide spectrum of light to control photomorphogenic responses (Briggs, 1993). Both red light, via phytochrome, and blue light, via blue/UV photoreceptor(s), are effective in inducing photomorphogenic responses (Barnes and Bugbee, 1991; Cosgrove, 1981; Mohr, 1987). Light in the blue region of the spectrum has been associated with increased wheat tillering (Barnes and Bugbee, 1992) and floral induction in *Arabidopsis* (Eskins, 1992). The growth and seed production of plants grown under specific wavelengths and narrow bandwidth, therefore, must be characterized and understood before the acceptance of red LEDs as an alternative light source for growing plants in space. There are many studies which have examined photomorphogenic responses of plants to red and blue light from broad spectrum sources (Barnes and Bugbee, 1992; Britz and Sager, 1990; Eskins, 1992; Wheeler et al., 1991; Yorio et al., 1995) and LEDs (Brown et al., 1995; Bula et al., 1991, Hoenecke et al., 1992; Tennessen et al., 1994). A few studies have shown successful plant culture under red LEDs for various periods of time with species such as pepper [*Capsicum annuum* L.] (Brown et al., 1995), lettuce [*Lactuca sativa* L.] (Hoenecke et al., 1992), and kudzu [*Pueraria lobata* (Willd.) Ohwi.] (Tennessen et al., 1994). However, there is little information available on the use of LEDs to support plants through an entire life cycle.

The objectives of this study were (1) to determine the usefulness of red LEDs in growing wheat and *Arabidopsis* through one full generation producing viable seeds, and (2) to determine if

the addition of supplemental blue fluorescent radiation is beneficial for the germination, growth, and seed production of wheat and *Arabidopsis*.

MATERIALS AND METHODS

Cultural Conditions

Wheat

Wheat seeds (*Triticum aestivum* L. cv. Superdwarf) were imbibed in the dark on moistened germination paper for 72 h at 4°C followed by incubation at room temperature for 24 h. The newly germinated seedlings were transplanted into plastic pots (3-inch, 450 mL capacity, 12 seedlings/pot) containing soil-less media (Metro-Mix 220, Grace Sierra Co., Milpitas, CA). Within each of three growth chambers (Conviron PGW-36, Pembina, ND; 7.8 m³ interior plant growth volume), nine pots were arranged in a 3X3 configuration inside a 0.2 m² tray, under each light treatment. At 7 days after planting (DAP), the wheat seedlings were thinned to a density of 10 plants/pot. Growth chamber air temperature and relative humidity for all treatments were maintained at 23°C and 65%, respectively, and measured daily with a hand-held metering device (Vaisala HMI 31, Helsinki, Finland) at the top of the plant canopy. Fresh, 0.25X-strength, modified Hoagland's nutrient solution (Table 1) was added daily to the bottom of each tray to supply nutrients and replenish evapo-transpirative loss. To minimize border and positional effects within each 3X3 configuration, pots were systematically rotated every other day.

Arabidopsis

Approximately 10-20 *Arabidopsis* [*Arabidopsis thaliana* (L.) Heynh, race Columbia] seeds, in a water slurry, were pipetted on the surface of 5 cm ARABASKET pots (ARASYSTEM, Lehle Seeds, Tucson, AZ) containing moist Metro-Mix 220. Two ARAFLAT trays (each containing 7 ARABASKET pots), were placed in growth chambers under each respective light treatment (see above). Pots then were covered with clear plastic and sealed with a rubber band. At 5 DAP the pots were uncovered, and at 7-10 DAP the *Arabidopsis* seedlings were thinned to

one plant in each pot. Growth chamber air temperature and relative humidity for all treatments were maintained at 23°C and 65%, respectively, and checked daily with a hand-held metering device (Vaisala HMI 31, Helsinki, Finland). Plants were watered from the bottom daily with fresh, 0.25X-strength, modified Hoagland's nutrient solution (Table 1). To minimize border and positional effects within ARAFLAT trays, each tray was systematically rotated every other day.

Table 1. Salt concentration used in 0.25X-strength modified Hoagland's nutrient solution.

Salt	Concentration
Ca(NO ₃) • 4H ₂ O	2.5 mM Ca 5.0 mM N
KNO ₃	2.5 mM K 2.5 mM N
MgSO ₄ • 7H ₂ O	1.0 mM Mg 1.0 mM S
KH ₂ PO ₄	0.5 mM K 0.5 mM P
FeCl ₃ • 6H ₂ O + HEDTA	50 µM Fe 150 µM Cl 47 µM HEDTA
H ₃ BO ₄	4.75 µM B
MnCl ₂ • 4H ₂ O	3.70 µM Mn
ZnSO ₄ • 7H ₂ O	0.64 µM Zn
CuSO ₄ • 5H ₂ O	0.52 µM Cu
(NH ₄) ₆ Mo ₇ O ₂₄ • 4H ₂ O	0.01 µM Mo

Light Treatments

The four light sources were red LEDs only, red LEDs + 1% blue fluorescent (BF), red LEDs + 10% BF, and daylight fluorescent (white). Spectral distribution scans were taken (at equal photosynthetic photon flux, PPF) from 300 to 1100 nm in 2 nm steps with a spectroradiometer (Model LI-1800; LI-COR, Lincoln, NE) (Fig. 1). Contributions of blue (400-500 nm), red (600-700 nm), and total PPF (400-700 nm) were determined from bandwidth integration. For the red LED treatments, plants were grown under arrays (Fig. 2) equipped with red gallium-aluminum-

arsenide (GaAlAs) LEDs. The arrays were mounted in a 0.17m² ventilated enclosure and contained 2624 individual LED units for wheat or 1952 units for *Arabidopsis*. For the red + blue light supplemented treatments, blue fluorescent lamps (Philips 20-W F20T12/BB) were mounted around the LED arrays to supply approximately 10% or 1% of the total PPF, as determined by the quantum sensor (Model LI-189; LI-COR, Lincoln, NE) measurements at the top of the plant canopy. A vestibule made of black, non-transparent plastic precluded outside light from entering growth chambers which contained LED arrays. Control plants were grown under broad-spectrum daylight fluorescent lamps (Sylvania 115-W F48T12/D/VHO with a 3.5 mm-thick Plexiglas heat barrier) that provided approximately 28% PPF (Fig. 1) in the blue region of the spectrum (400-500 nm).

Lighting for all treatments was continuous (24 hour light/0 hour dark photoperiod) with equal amounts of PPF. The PPF levels were maintained at 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for wheat and 175 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for *Arabidopsis*. As the plant canopies grew closer to the light banks, the PPF levels were maintained by adjusting the height of the pots and/or adjusting input wattage on the power supplies for the LEDs (PD35-20D; Kenwood Corp., Tokyo) and BF lights (Model No. FX0696-4, Mercron, Richardson, TX). The PPF levels were measured daily at the top of the plant canopy with a quantum sensor. The daylight fluorescent light bank and the array with red LEDs alone were in separate growth chambers. The red LED arrays supplemented with 1% or 10% blue light were located in the same growth chamber. The red + 1% BF light bank was positioned on the upper tier of the same rack immediately above the red + 10% BF light bank.

Plant Growth Measurements

Wheat

Plant growth measurements for wheat were recorded at each destructive harvest to coincide with the following growth stages: vegetative (15 DAP), pre-anthesis (25 DAP), grain fill (40 DAP), and senescence (70 DAP). Measurements at 15, 25, and 40 DAP included the following parameters: plant height, tiller number, tiller fresh weight, total plant fresh weight and dry weight, and leaf net photosynthesis (Table 2). Plant height was determined as the distance between the plant stem base to the tip of the longest extended leaf. Net photosynthesis was calculated from the measured rate of CO₂ uptake (Model LI-6200, LI-COR, Lincoln, NE) by the youngest fully expanded leaf (15 and 25 DAP) or flag leaf (40 DAP). Flag leaf length was measured at 40 DAP. Harvested plant tissue was weighed before and after drying in an oven at 70°C for 48 h.

For each treatment, final harvest occurred at 70 DAP, when the flag leaves were senescent and the main culm heads were dry. The following measurements were made at final harvest: plant height, tiller number, total vegetative fresh and dry weight, tiller head number, tiller head fresh and dry weight, main culm head fresh and dry weight, and seed number and dry weight (Table 2). Tiller and main culm heads were dried by storing them in a sealed plastic bag containing desiccant (anhydrous CaSO₄, Drierite Co., Xenia, OH).

Growth data at 15, 25, and 40 DAP represent averages of 12 plants from two replicated runs of the experiment (Table 2). At 70 DAP, growth data represent averages of 30 plants from three replicated runs of the experiment. Using 5% and 10% as the levels of significance, all growth data were subjected to analysis of variance (ANOVA, SAS Institute, 1990). Mean separation was by Duncan's multiple range test.

To compare the radiation conversion efficiency of the light sources, seed yield (g) was calculated per unit energy consumed (megajoules) in the following way: The energy consumption during the course of the wheat life cycle (70 days) was converted to megajoules (MJ) PAR (photosynthetically active radiation) by dividing 350 μmol m⁻² s⁻¹ by the appropriate constant (4.6 for fluorescent; 5.6 for red LEDs) to obtain W m⁻² (Deitzer, 1994). Values for W m⁻² were then

multiplied by the growing area used in each chamber (0.186 m^2) and the total irradiation time (seconds) for the wheat life cycle, to obtain the amount of energy (Joules) provided.

Germination tests were performed after seeds were stored at 4°C in the presence of desiccant for at least 30 d post-harvest. Twenty dry seeds per treatment were incubated on water-moistened germination paper in parafilm-sealed Petri dishes at 4°C for 72 h. Petri dishes were wrapped with aluminum foil to preclude light. Petri dishes then were transferred to 23°C for 24 h, and seeds which displayed an emerged radicle were counted as germinated.

Table 2. Summary of wheat plant growth measurements along with time of measurements, number of replicated experiment runs, and number of plants measured for each treatment within each replicated experiment run.

DAP	Measurement	Replicated Experiment Runs	No. of Plants Measured Per Treatment
15, 25, and 40	plant height	2	6
	tiller number	2	6
	tiller fresh weight	2	6
	total plant fresh weight	2	6
	total plant dry weight	2	6
	net photosynthesis	2	6
40	flag leaf length	2	6
70	plant height	3	10
	tiller number	3	10
	total vegetative fresh weight	3	10
	total vegetative dry weight	3	10
	tiller head number	3	10
	tiller head fresh weight	3	10
	tiller head dry weight	3	10
	main culm head fresh weight	3	10
	main culm head dry weight	3	10
	seed number per plant	3	10
	seed yield per plant	3	10
	dry weight per seed	3	10
post-harvest	radiation conversion efficiency	3	10
	seed germination rate	3	20 seeds

Arabidopsis

Plant growth measurements recorded for *Arabidopsis* included rosette leaf number, area, fresh weight, and dry weight at 20 DAP (Table 3). At 40 DAP, these same leaf measurements were recorded along with floral stalk number, length, fresh weight, and dry weight. Also at 40 DAP, siliques number per plant, longest siliques length, and seed number per longest siliques were recorded. Rosette ground cover area was determined from digitized images of the plants using a public domain image program (National Institutes of Health, Springfield, VA). Seed number per plant was calculated by multiplying the total number of siliques per plant by the number seeds found in the longest siliques. Growth data for *Arabidopsis* represent the averages of 14 plants at 20 DAP, and 7 plants at 40 DAP. An additional 7 plants under the array with red LEDs alone were allowed to complete seed set which occurred at approximately 60-70 DAP.

Table 3. Summary of *Arabidopsis* plant growth measurements along with time of measurements and number of plants measured for each treatment.

Days After Planting	Measurement	No. of Plants Measured Per Treatment
20	rosette leaf number	14
	rosette ground cover area	14
	rosette fresh weight	14
	rosette dry weight	14
40	rosette leaf number	7
	rosette ground cover area	7
	rosette fresh weight	7
	rosette dry weight	7
	siliques number per plant	7
	floral stalk number	7
	floral stalk length	7
	floral stalk fresh weight	7
	floral stalk dry weight	7
	longest siliques length	7
post-harvest	seed number in longest siliques	7
	seed germination rate	20 seeds

For seed germination tests, 2 ARAFLAT trays were sown (as described above) with 20 seeds generated from each set of *Arabidopsis* mother plants grown under the respective light treatments. One ARAFLAT tray was placed under white light, while the other tray was placed under red LEDs alone at the same light level and environmental conditions as described above. After 4 days, germinated seedling counts were performed.

RESULTS AND DISCUSSION

Wheat

Throughout the life cycle, plant height for wheat was similar between light treatments (Fig. 3). However, flag leaf length (at 40 DAP) was greatest when wheat was grown under red LEDs without supplemental blue light (Fig. 3, inset). Flag leaves from plants grown with red LEDs + 1% or 10% BF were not significantly different from flag leaves from the control wheat. At 15 DAP, total fresh weight ($P<0.1$) and dry weight ($P<0.05$) were significantly greater in the control wheat than in wheat grown in the presence of red LEDs alone (Figs. 4, 5). At 25 and 40 DAP, control wheat again had a higher total fresh weight and dry weight than did wheat grown under red LEDs alone, although treatment differences were not statistically different due to large plant to plant variation at these particular growth stages. Compared to wheat grown under red LEDs alone, 1% supplemental BF light appeared to have little to no effect on fresh and dry weight accumulation. However, at 25 and 40 DAP, wheat grown under red LEDs + 10% BF light showed some increase in total fresh and dry weight accumulation when compared to wheat grown under red LEDs alone.

At 15 and 40 DAP, wheat grown under white light showed no statistical difference from wheat grown under red LED + 10% BF light in terms of leaf net photosynthesis. However, wheat grown under white light or red LED + 10% BF light at 15 and 40 DAP had a significantly higher rate of net photosynthesis than wheat grown under red LEDs alone or under red LEDs + 1% BF light. At 25 DAP, white light-grown wheat had a significantly higher rate of leaf net photosynthesis than wheat grown under all treatments involving red LEDs (Fig. 6). Hence, our data on leaf net photosynthesis corresponded closely to the fresh and dry weight data, where red

LEDs + 10% BF light produced wheat with growth characteristics that were often similar to the white light-grown wheat. In another study that compared red LEDs with white light-grown plants, photosynthesis in kudzu was greater under red LEDs at low light intensities, lower at high intensities, and equal at saturating CO₂ levels (Tennesen et al., 1994). Lower photosynthesis in plants under red LEDs, as opposed to white light, may be associated with lower stomatal conductance (Farquhar and Sharkey, 1982). Stomates have been shown to be more responsive to blue light than red light (Sharkey and Raschke, 1981). In our study, photosynthesis increased as the level of blue light increased, which may suggest that stomatal conductance was a factor limiting photosynthetic rates under red LEDs. Although flag leaf stomatal index was not different among light treatments, initial flag leaf steady-state porometry measurements showed that stomatal conductance correlated closely with net flag leaf photosynthesis.

Wheat grown under red LEDs alone, or with 1% BF light, also had the lowest number of tillers per plant (Fig. 7) and tiller fresh weight per plant (Fig. 8). This result is in agreement with previous studies where wheat produced more tillers with increasing amounts of blue light, provided that the phytochrome balance (ϕ) was held constant (Barnes and Bugbee, 1991, Barnes and Bugbee, 1992). However, it is uncertain whether photomorphogenic responses to blue light are interdependent (Mohr, 1987) or independent (Cosgrove, 1981) of the phytochrome response (Mohr, 1987). The number of tillers that produced heads, and the tiller head dry weight were greater for control plants than for any of the red LED treatments (Fig. 9), although treatment differences were not statistically different due to large plant to plant variation within treatments. Wheat in the presence of red LEDs + 1% BF light were the only plants that failed to produce seed bearing tillers. The potential photoassimilate contribution from tillers that did not bear seed is uncertain, and such tillers may even become undesirable for optimizing seed yield and harvest index (Rawson and Donald, 1969; Bugbee and Salisbury, 1988).

At final harvest (70 DAP), vegetative fresh and dry weight mostly followed the same trends observed between 15 and 40 DAP. Fresh weight (P<0.1) and dry weight (P<0.05) of seed heads and total plant dry weight (P<0.1) were significantly greater for control wheat than for wheat grown with red LEDs alone or with red LEDs + 1% BF light (Figs. 10, 11). However, when

wheat was grown in the presence of red LEDs + 10% BF light, total dry weight accumulation was not significantly different from the control wheat at final harvest. All treatments successfully produced mature seed at final harvest (Figs. 12, 13). However, wheat grown under red LEDs alone, or with 1% BF light, had a significantly lower seed yield ($P<0.05$; Fig. 13), dry weight per seed ($P<0.05$; Fig. 14), and seed number per plant ($P<0.1$; Fig. 14) than control wheat.

Establishing a direct relationship between photosynthesis and seed yield is difficult due to the multitude of other factors that influence yield (Simmons, 1987). Photosynthesis and photoassimilate partitioning may have some relationship to spectral quality of the light source (Britz and Sager, 1990). Indirect evidence from studies on shading, thinning, and leaf area correlation suggests that photosynthesis is important for seed yield in wheat (Fischer, 1975; Fischer and Laing, 1976). In our study, higher net photosynthetic rates in white light-grown plants could have produced greater resource allocation pools than in the less photosynthetically active red LED-grown plants. The control wheat reached early boot stage (beginning of reproductive spike development) at approximately 28 DAP, while the wheat under the red LED treatments showed signs of booting between 33 and 36 DAP. Disproportionate net photosynthetic rates (Fig. 6) along with a 5-8 day difference in the initiation of spike development among treatments could have contributed to the observed difference in dry weight partitioning patterns (Figs. 10, 11). Higher net photosynthesis coupled with an earlier boot stage may have given the control wheat a longer period of time between grain fill and senescence to allocate photoassimilates to reproductive tissues. As much as 90% of wheat seed yield may be derived from photoassimilates produced after anthesis (Austin et al., 1977).

Wheat grown under red LEDs + 1% BF and red LEDs alone had the lowest radiation conversion efficiency (seed yield per unit energy consumed by the light source expressed as $\text{g}\cdot\text{MJ}^{-1}$ PAR) as determined by the apparatus and conditions specific for this study. Radiation conversion efficiency was highest in control wheat, followed closely by wheat grown in the presence of red LEDs + 10% BF (Fig. 13). Because of their wavelength specificity, the utilization of blue LEDs instead of blue fluorescent lamps may improve the radiation conversion efficiencies of the red LED treatments employed in this study. Additional energy savings may be accomplished

with all of the lighting sources used in this study through integration of reflective materials and more attention to side lighting. However, it is important to note that maximizing radiation conversion efficiency was not the main focus of this study.

With the recent developments in blue LED technologies, it appears that red LEDs in combination with blue LEDs, instead of fluorescent lighting, could bolster advantages gained through LED safety, ruggedness, and possibly power consumption. It is clear from the results of this study that supplemental radiation in the blue region of the spectrum is an important factor contributing to normal development, growth, and physiology of wheat when using red LEDs. Overall, in terms of photomorphogenesis and seed yield, our results suggest that wheat grown under red LEDs require supplemental BF light greater than $3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in order to be comparable to wheat grown under white light.

Seed germination was greatest (92%) for wheat grown under red LEDs + 1% BF light, and least (75%) for seed from the control wheat (Fig. 13, inset). Wheat grown under red LEDs + 1% or 10% BF light had significantly greater germination rates than wheat grown under white light or red LEDs alone. Because of post-harvest dormancy, germination counts from this study may be lower than the actual number of viable seed produced. For the same reason, germination counts may improve beyond what we report here, if a longer storage period is allowed before performing germination tests. Superdwarf wheat has been reported to require at least 6 months of storage to overcome post-harvest dormancy (Anderson et al., 1995).

Arabidopsis

In *Arabidopsis*, the proportion of vegetative versus reproductive dry weight in the total plant shoot was affected by different light regimes. At 20 DAP, *Arabidopsis* grown under red LEDs alone displayed marginally lower rosette fresh weight (Fig. 15), dry weight (Fig. 16), and ground cover area (Fig. 17) than *Arabidopsis* grown under all the other light regimes. However, by 40 DAP, *Arabidopsis* grown under red LEDs alone had much greater rosette fresh weight (Fig. 15), dry weight (Fig. 16), and ground cover area (Fig. 17) than was observed under the other light

treatments. Under red LEDs alone, only a few *Arabidopsis* plants had initiated floral development at 40 DAP as opposed to plants under the other light treatments, where a large portion of their photoassimilates was allocated to floral and seed structures by this time. Hence, at 40 DAP, under red LEDs alone, *Arabidopsis* partitioned essentially all photoassimilate into vegetative growth (Figs. 18, 19), as indicated by the high number of rosette leaves (Fig. 20), rosette dry weight (Fig. 16), and lack of floral stem development (Fig. 20, inset). These findings agree with a previous study (Eskins, 1992) where leaf area decreased as the proportion of blue light relative to total irradiance increased.

Interestingly, *Arabidopsis* plants grown in the presence of red LEDs alone developed unusual growth patterns beginning at germination (see seed germination rate results below). By 10 DAP, *Arabidopsis* plants under red LEDs alone displayed leaves that cupped downward, and by 20 DAP these same leaves had downward curled margins (Fig. 21). Also, entire leaves grew in a spiraling direction around the central plant axis under red LEDs alone (Fig. 21). Superdwarf wheat under red LEDs alone did not show any such morphological abnormalities (Fig. 12). Unusual growth patterns persisted throughout the life cycle of *Arabidopsis* under red LEDs alone, even as those plants developed additional leaves. The unusual leaf curvature appears to be a response to the absence of blue light, because 1% BF light nullified this condition (Fig. 21). Previous studies have shown increased elongation of hypocotyls, cotyledons, and stems induced by blue light-deficient sources can be offset by the addition of supplemental blue light (Brown et al., 1995; Hoenecke et al., 1992; Wheeler et al., 1991; Yorio et al., 1995).

The effect of light quality on flowering has been measured as the number of days until bolting (Eskins, 1992). In this study, initiation of bolting was defined as when at least one bolting stalk had appeared in each pot. *Arabidopsis* displayed bolting floral stems at 20 DAP when grown under daylight fluorescent light (Fig. 20, inset). *Arabidopsis* grown under red LEDs developed floral stems progressively later (between 2-15 days later), as the amount of supplemental BF light decreased. *Arabidopsis* grown under white light, as well as *Arabidopsis* grown under red LEDs + 10% BF, had the greatest floral stem length at 40 DAP. At 70 DAP, *Arabidopsis* under red LEDs

alone produced floral stem length comparable to observations at 40 DAP of the other treatments (Fig. 22).

The spectral quality of light has been shown to have an important effect on floral initiation and morphology of *Arabidopsis* (Eskins, 1992; Goto et al., 1991; Martínez-Zapater et al., 1994). Red light had a strong inhibitory effect on floral transition in this study, which suggests that the P_{fr} form of phytochrome and/or the absence of blue light may have repressed floral transition (Eskins, 1992; Goto et al., 1991). Phytochrome equilibrium may not be the sole regulator of photomorphogenesis and flowering in *Arabidopsis*. Initiation of flowering in *Arabidopsis* has been shown to be directly related to the irradiance level of blue light, provided that the phytochrome photoequilibrium (P_{fr}/P_{tot}) is held constant (Eskins, 1992). Blue- and far-red-mediated responses may involve different pathways (Eskins, 1992), or blue light may interact synergistically with phytochrome to mediate photomorphogenic responses and initiate flowering (Barnes and Bugbee, 1991; Cosgrove, 1981; Esskins, 1992; Mohr, 1987).

At 40 DAP, siliques on the white light-grown *Arabidopsis* had already begun to dehisce, indicating that siliques had reached maturity. Conversely, *Arabidopsis* grown under red LEDs alone required approximately 60 to 70 days to produce mature siliques (Fig. 23). At 40 DAP, all light regimes except the red LEDs alone had produced viable seed. *Arabidopsis* grown under white light produced significantly more siliques per plant (Fig. 22), longer siliques (Fig. 24), and more seeds per plant (Fig. 25) than were observed in each of the red LED treatments. Although seed production was less than observed under white light, the addition of 10% blue light to the red LEDs increased seed production in *Arabidopsis*, surpassing seed production achieved in plants grown under red LEDs + 1% BF or red LEDs alone (Fig. 25). *Arabidopsis* grown under red LEDs alone eventually set seed but required approximately 60-70 DAP, whereas the other treatments had various amounts of viable seed produced by 40 DAP. These results suggest that blue light shifts *Arabidopsis* towards reproductive activity, and red light promotes vegetative growth. Our results are consistent with a previous study where plants grown in red light were vegetative and large, but plants grown in blue light had less vegetative mass but were quicker to flower and set seed (Eskins, 1992).

Seed from *Arabidopsis* grown under each light treatment germinated with at least a 93% germination rate under white light and at least a 85% germination rate under red LEDs (Fig. 25, inset). After 5 days, seedlings that germinated under red LEDs alone had downward cupped leaves and elongated hypocotyls. Despite this condition, chlorophyll development appeared normal in seedlings germinated under red LEDs alone. Cupped leaves and elongated hypocotyls were present in all seedlings irrespective of the mother plant. All of the seedlings that germinated under white light appeared normal. Hypocotyl elongation under red LEDs alone may have resulted from the lack of blue light, because blue light has been shown to inhibit hypocotyl elongation in *Arabidopsis* (Liscum and Hangarter, 1991). Previous work has indicated that spectral composition of the light source during growth of *Arabidopsis* plants may influence the sensitivity of the seeds to red-light-induced germination (Hayes and Klein, 1974; McCullough and Shropshire, 1970). However, there was no clear indication in this study that any of the light treatments affected germination of the seeds taken from the respective mother plants.

SUMMARY

Wheat

1. Wheat completed a normal life cycle and produced a greater percentage of viable seeds under all light regimes.
2. Wheat (a monocot) had normal morphology under red LEDs alone.
3. Wheat grown under red LEDs alone (without supplemental blue light) or red LEDs + 1% BF (blue fluorescent) light accumulated less total plant fresh weight and dry weight than plants grown under white light or red LEDs + 10% BF light.
4. Wheat grown under red LEDs with supplemental 10% BF light had seed yields similar to yields obtained under white light. When grown under red LEDs alone or red LEDs + 1% BF light, wheat had lower seed dry weight yields than plants grown under white light or red LEDs + 10% BF light.
5. Radiation conversion efficiency (seed yield per unit energy consumed by the light source) was greatest in white light-grown wheat, followed closely by wheat grown in the presence of red LEDs + 10% BF light. Radiation conversion efficiency was least under red LEDs + 1% BF light and red LEDs alone.
6. Overall, our results suggest that wheat grown under red LEDs requires supplemental BF light greater than $3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in order to be comparable to plants grown under white light, in terms of photomorphogenesis and seed yield.

Arabidopsis

1. *Arabidopsis* (a dicot) grown under red LEDs alone (without supplemental blue light) had abnormal leaf morphology. Normal leaf morphology was observed in the other treatments.
2. *Arabidopsis* grown under red LEDs alone or red LEDs + 1% BF (blue fluorescent) light accumulated less total plant fresh weight and dry weight than those plants grown under white light or red LEDs + 10% BF light.
3. *Arabidopsis* grown under red LEDs alone had seed set delayed by 20-30 days from a normal life cycle (approximately 35-40 days under white light).
4. Seed number and seed dry weight were lower in *Arabidopsis* grown under red LEDs alone or red LEDs + 1% BF than plants grown under white light or red LEDs + 10% BF light.
5. A high percentage of viable seeds were produced by *Arabidopsis* under all light regimes.

RECOMMENDATIONS FOR FUTURE FOLLOW-UP STUDIES:

- 1 . Test blue LED technology as an adequate source of blue radiation with red LEDs.**
- 2 . Determine threshold (absolute requirement) of blue light necessary to maximize radiation conversion efficiency.**
- 3 . Conduct LED life cycle studies on other plant species which will be flown in space.**
- 4 . Determine critical time period(s) that blue light is required within a life cycle to conserve power while maintaining normal plant growth and yield.**
- 5 . Compare LEDs and fluorescent light within the constraints of spaceflight hardware.**

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FIGURES

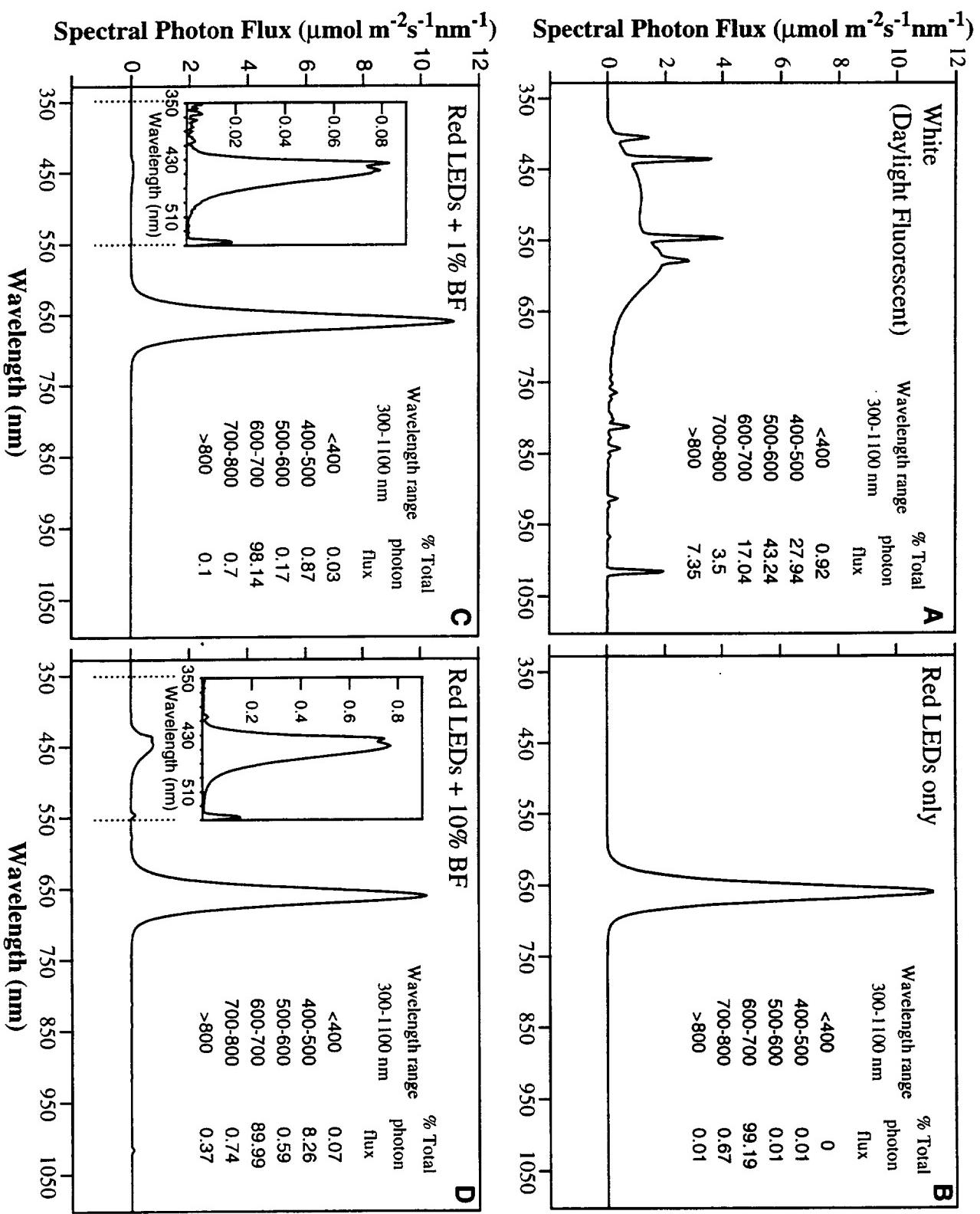


Fig. 1. Spectral distribution (300–1100 nm) of light from (A) daylight fluorescent lamps, (B) red light-emitting diodes (LEDs), (C) red LEDs + 1% blue fluorescent (BF) lamps, and (D) red LEDs + 10% BF lamps. Spectral scans were recorded at the top of the plant canopy with a spectroradiometer. Total PPF was approximately 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for all treatments.



Fig. 2. Superdwarf wheat plants growing under an array of red LEDs.

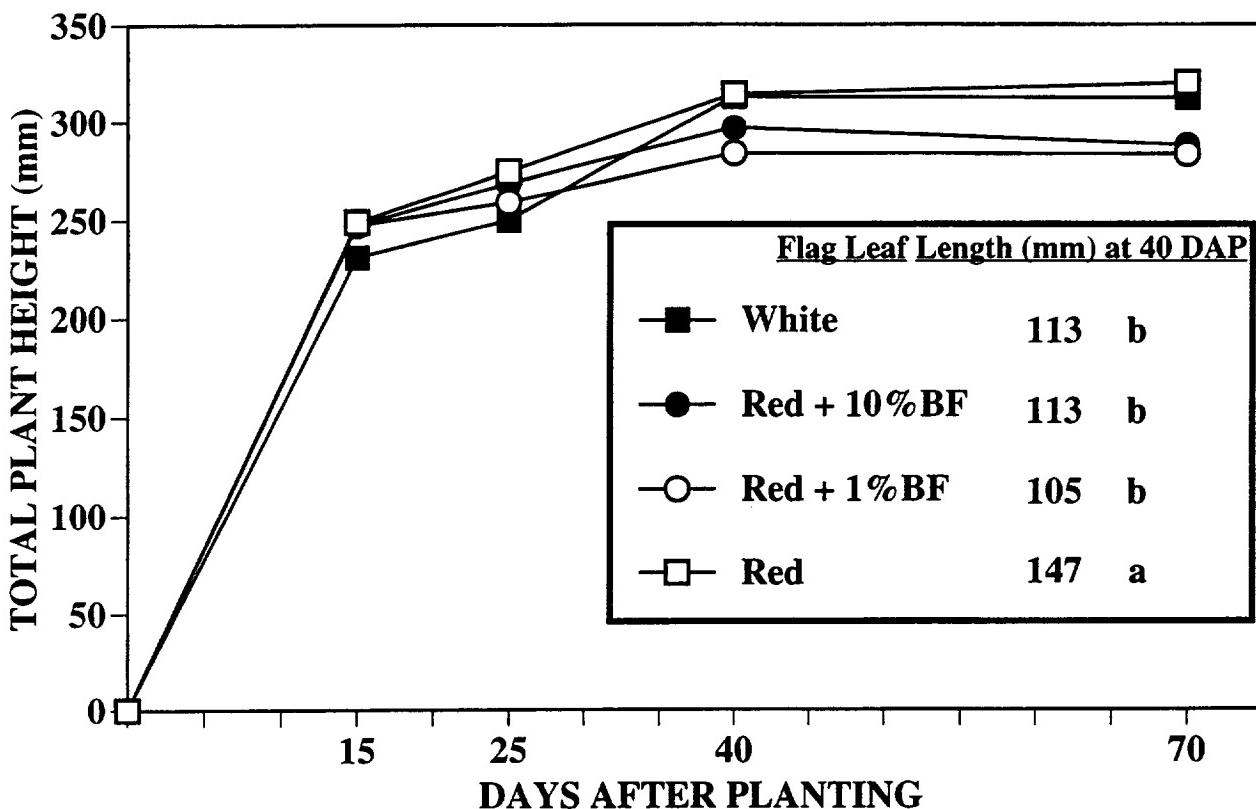


Fig. 3. Wheat height (graph) during 70 days and flag leaf (inset) length after 40 days in the presence of white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light. Data followed by different letters are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$).

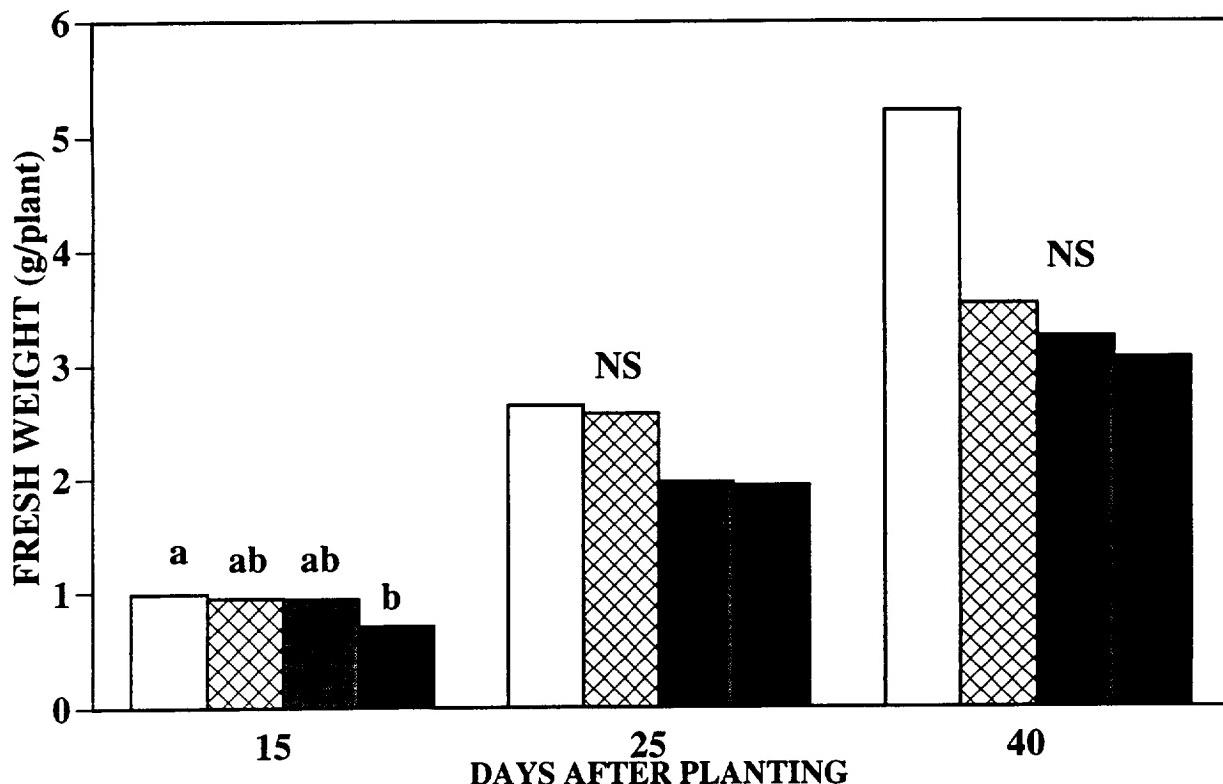


Fig. 4. Shoot fresh weight of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 15, 25, and 40 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.1$). NS denotes not significant at the 1% probability level.

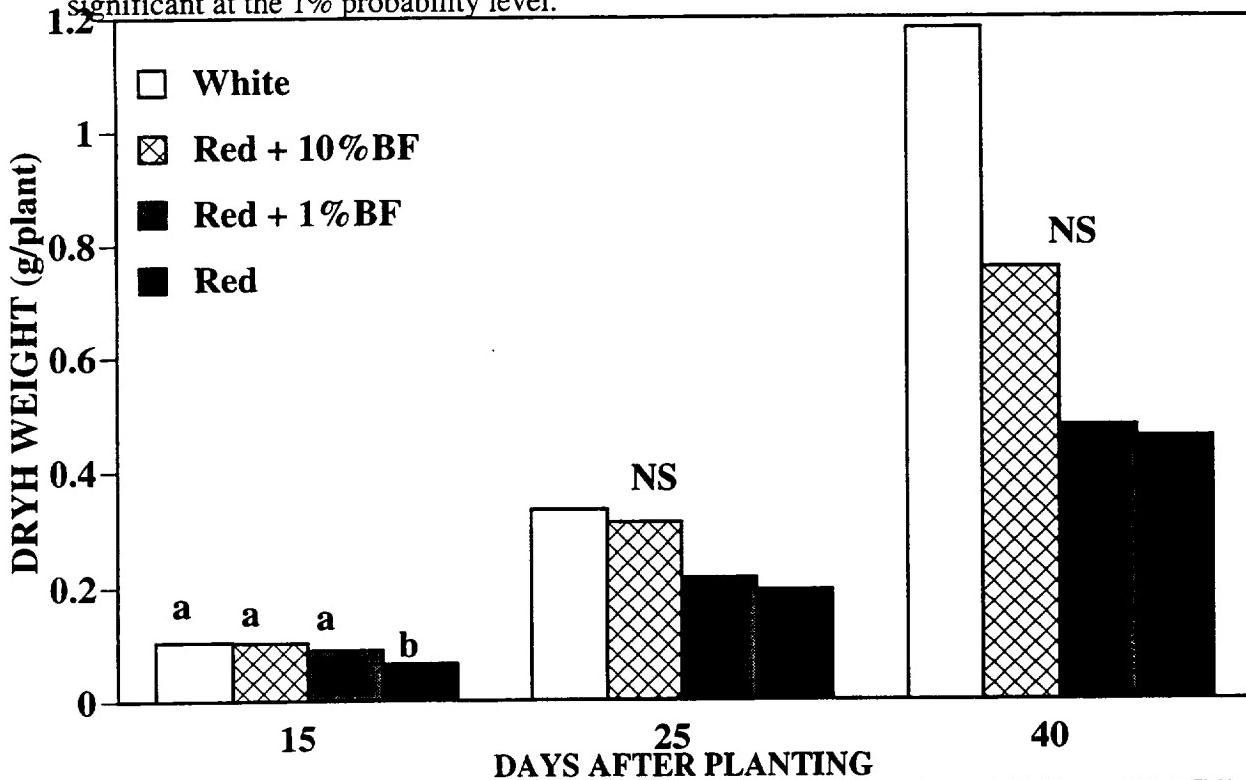


Fig. 5. Shoot dry weight of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 15, 25, or 40 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). NS denotes not significant at the 1% probability level.

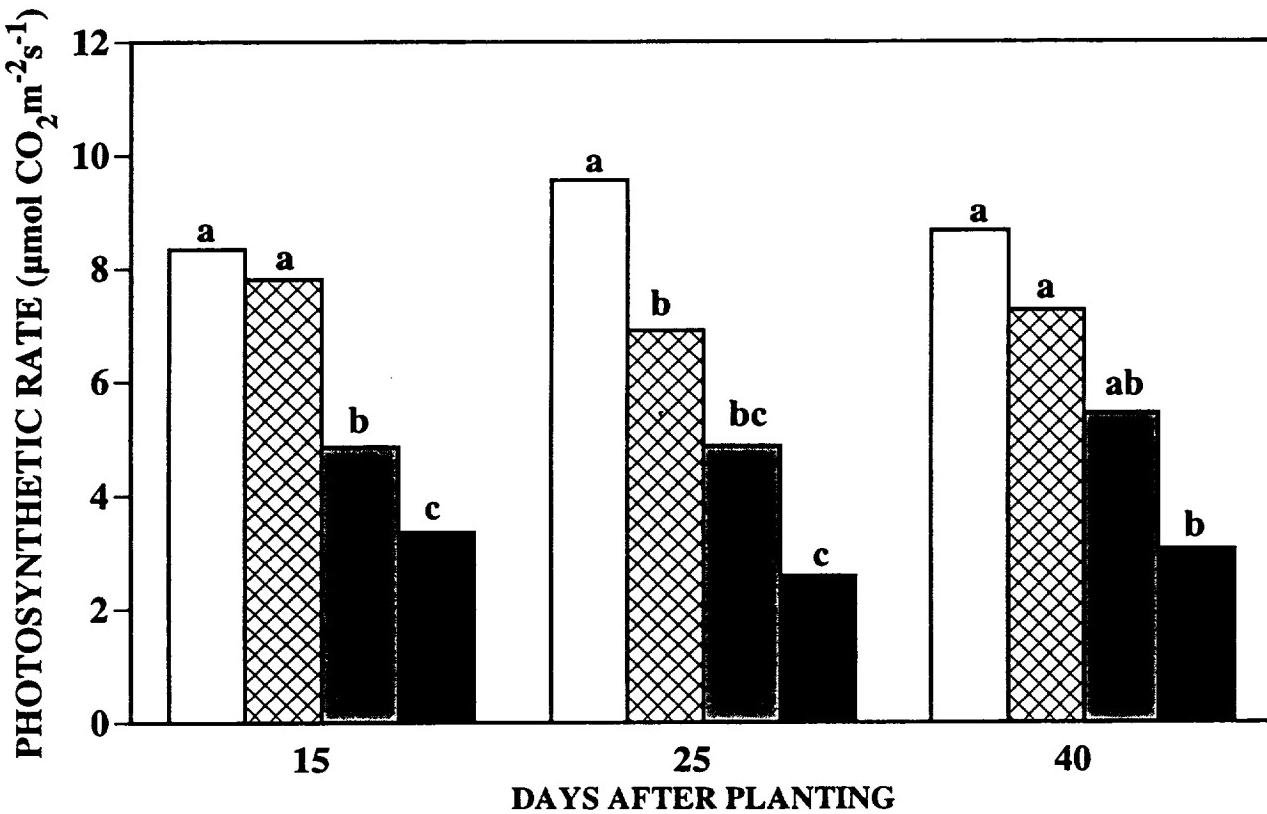


Fig. 6. Net rate of leaf photosynthesis of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 15, 25, or 40 days. Data points followed by different letters are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$).

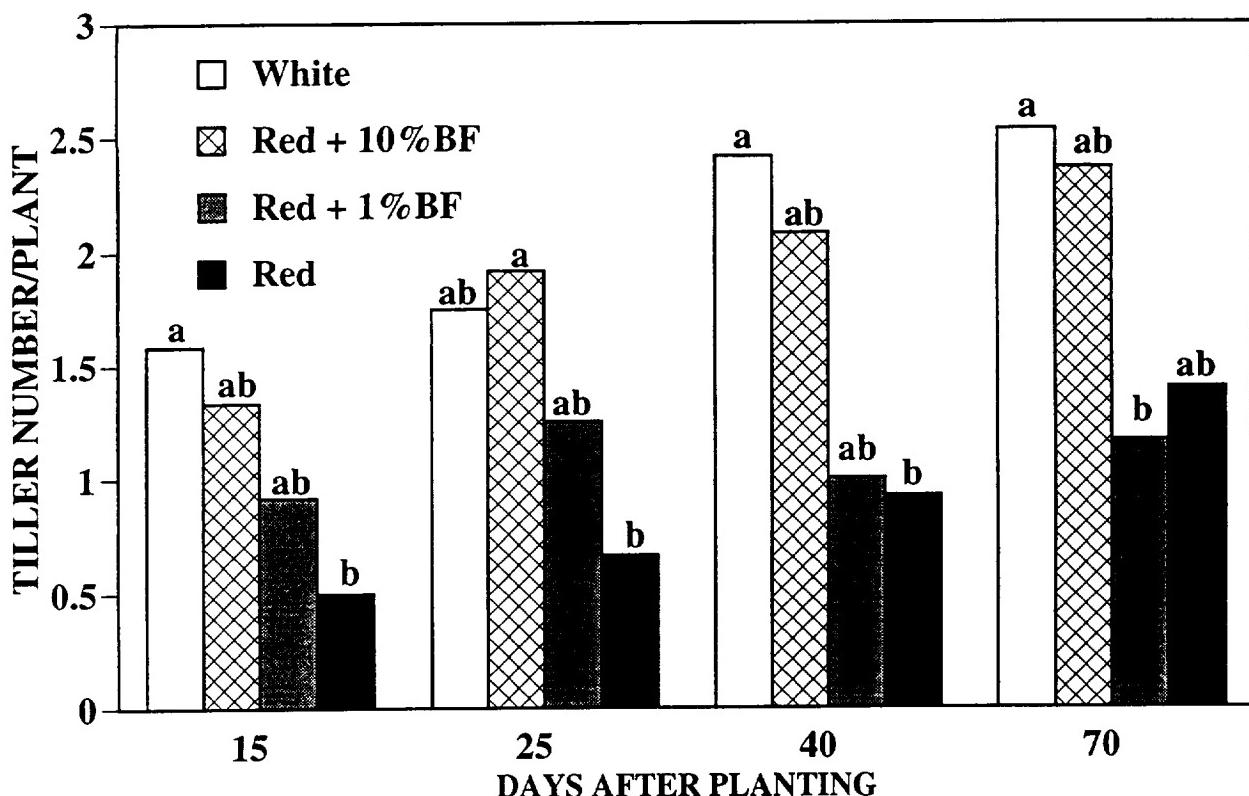


Fig. 7. Number of tillers produced by wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 15, 25, 40 or 70 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.1$).

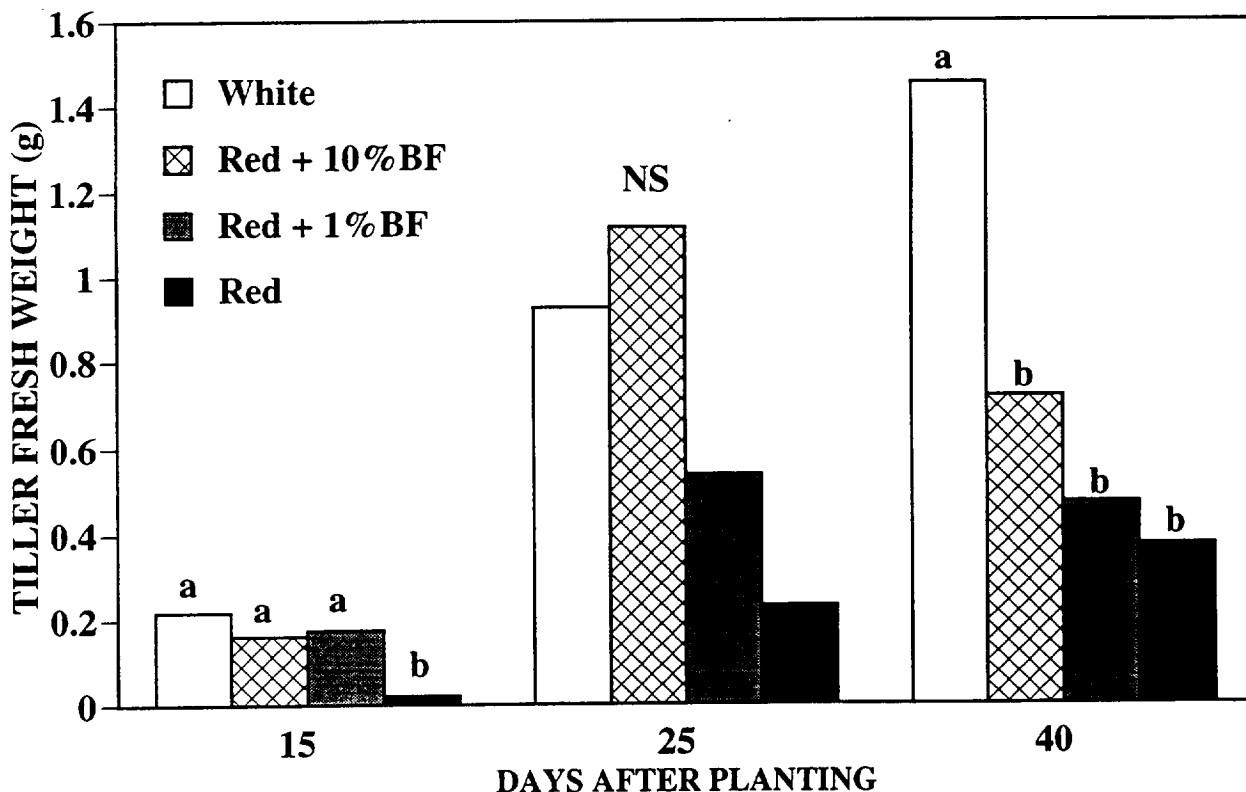


Fig. 8. Tiller fresh weight of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 15, 25, or 40 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). NS denotes not significant at the 1% probability level.

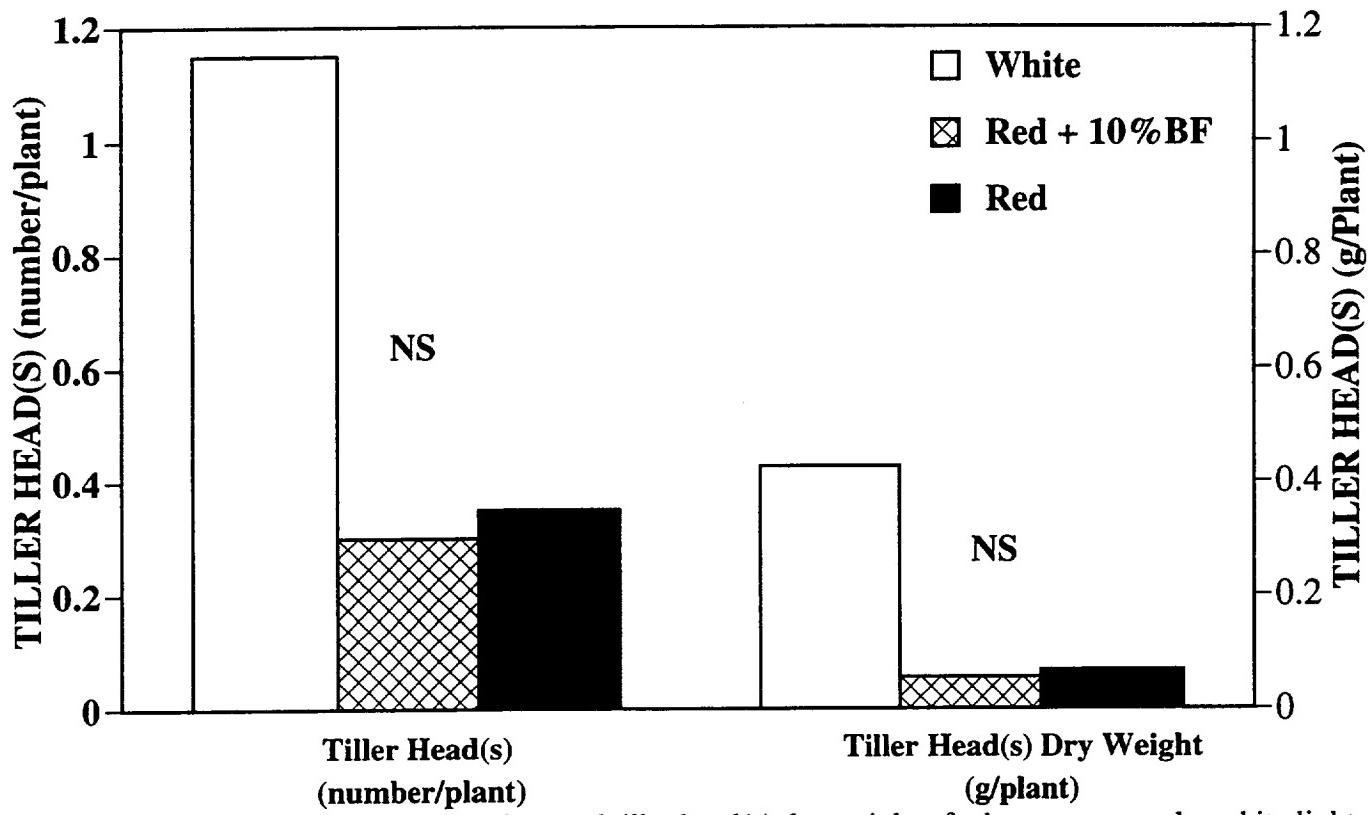


Fig. 9. Number of tiller head(s) per plant and tiller head(s) dry weight of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 70 days. NS denotes not significant at the 1% probability level based on ANOVA and Duncan's multiple range test. Wheat grown under red LEDs + 1% BF did not produce tillers with heads.

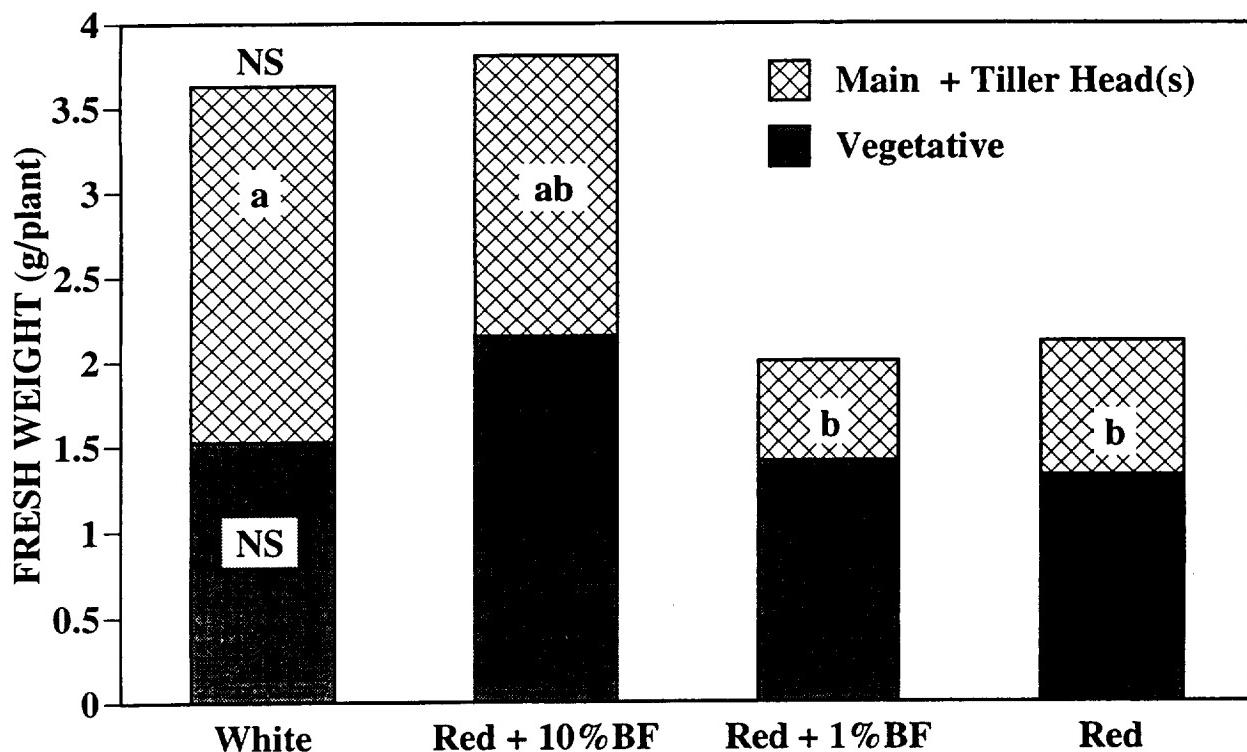


Fig. 10. Vegetative, main culm head, and tiller head(s) fresh weight of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 70 days. Similarly shaded portions containing different letters are significantly different based on ANOVA and Duncan's multiple range test ($P<0.1$).

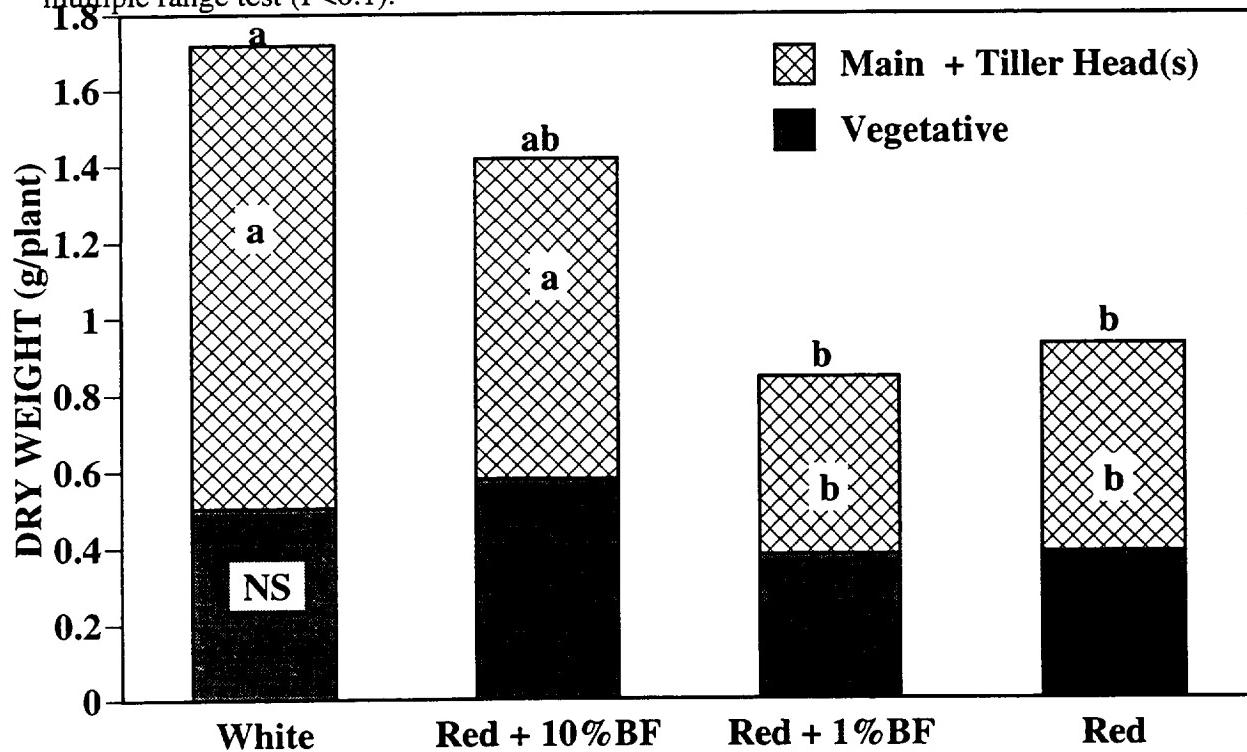


Fig. 11. Vegetative, main culm head, and tiller head(s) dry weight of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 70 days. Similarly shaded portions containing different letters are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). The letters above the bars indicate the significance for the combined plant dry weight ($P<0.1$).

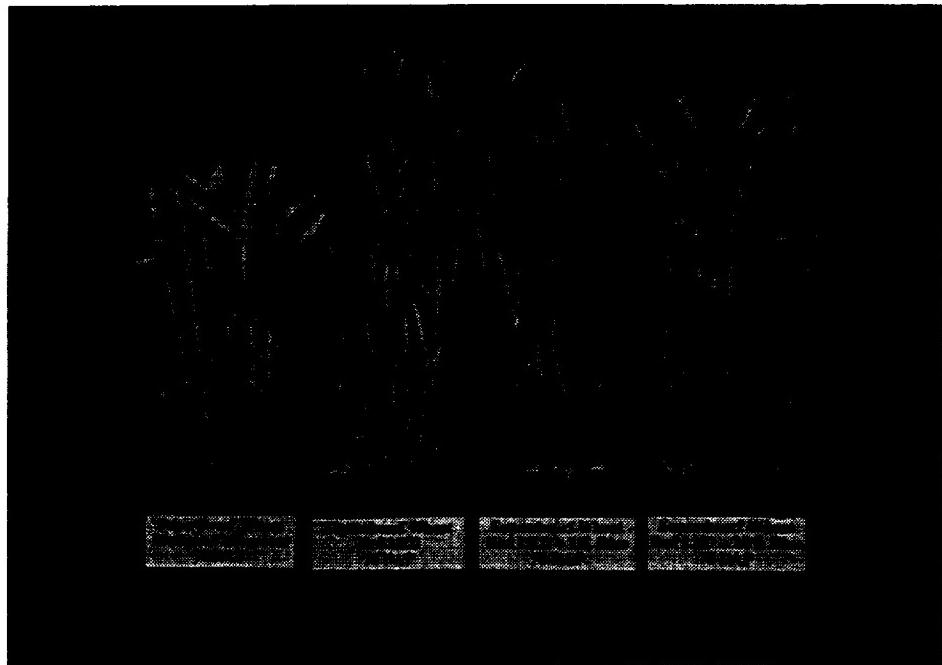


Fig. 12. Superdwarf wheat plants (10 plants/pot) from white light, red LEDs only, red LEDs + 1% BF light, or red LEDs +10% BF light at 70 DAP.

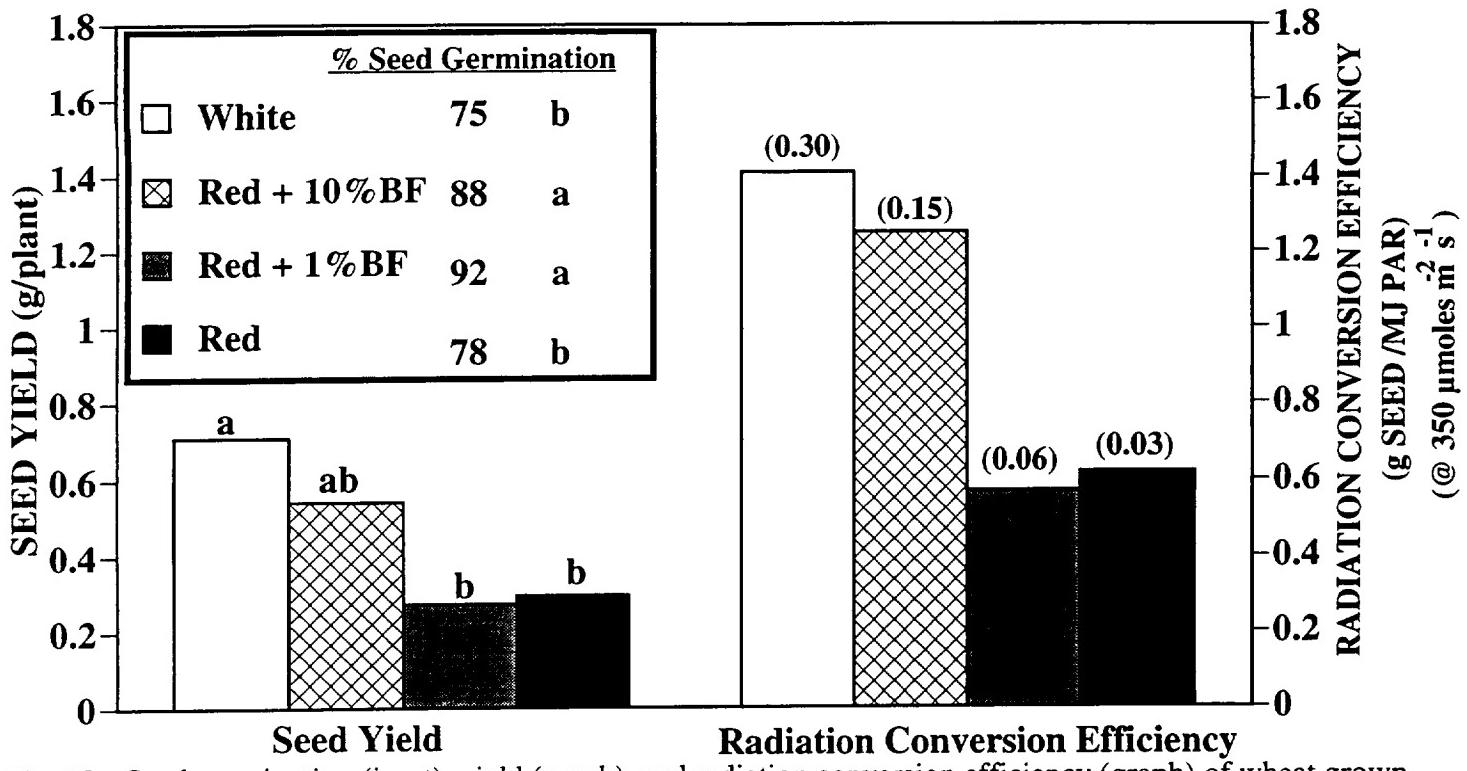


Fig. 13. Seed germination (inset), yield (graph), and radiation conversion efficiency (graph) of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 70 days. Bars and data with different letters within each type of measurement are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). Numbers in parentheses indicate standard error of the mean.

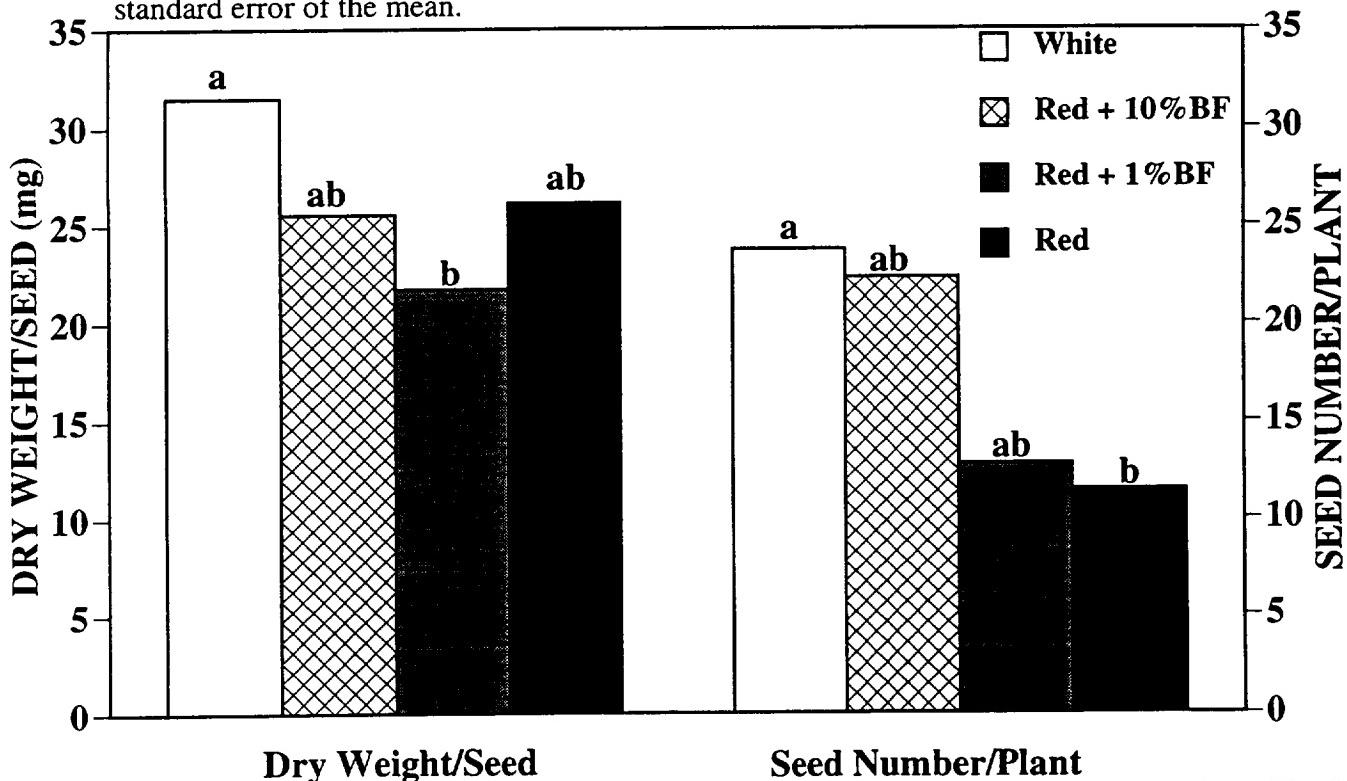


Fig. 14. Dry weight per seed ($P<0.05$) and seed number per plant ($P<0.1$) of wheat grown under white light, red LEDs only, red LEDs + 1% BF light, or red LEDs + 10% BF light for 70 days. Bars with different letters within each type of measurement are significantly different based on ANOVA and Duncan's multiple range test.

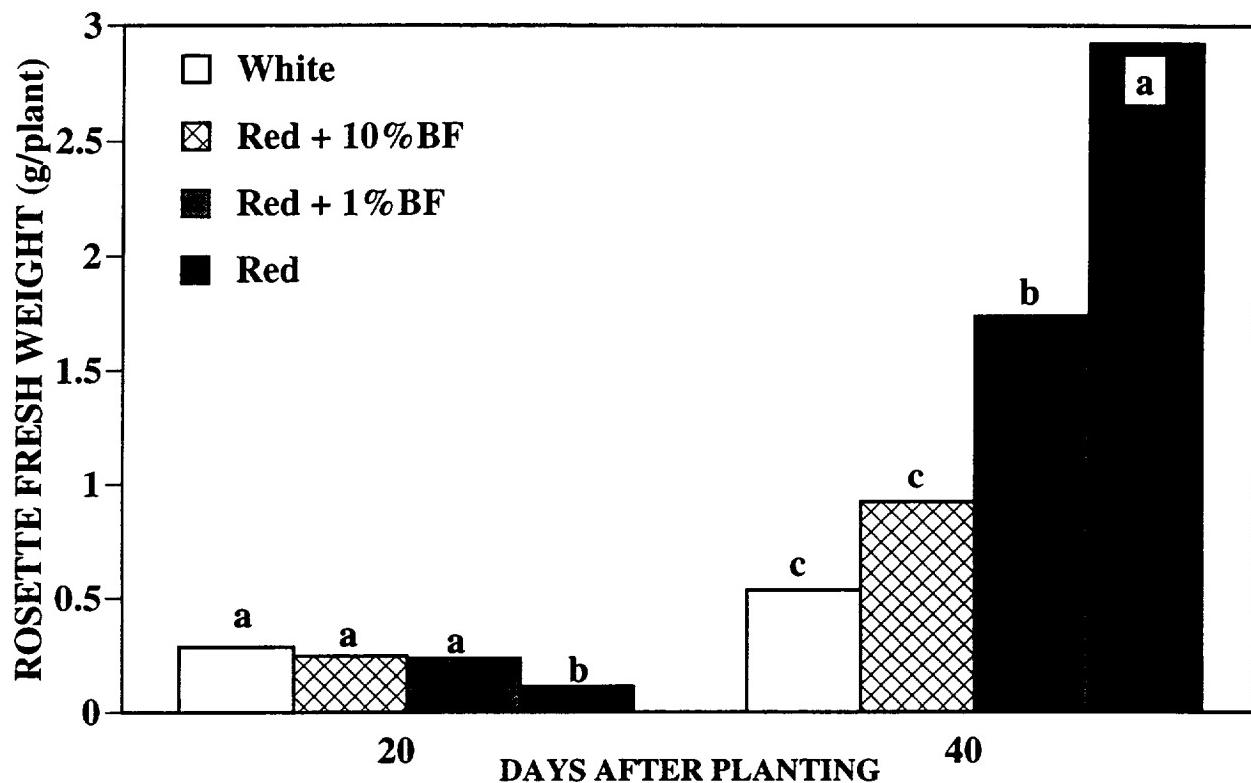


Fig. 15. Rosette fresh weight of *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 20 or 40 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$).

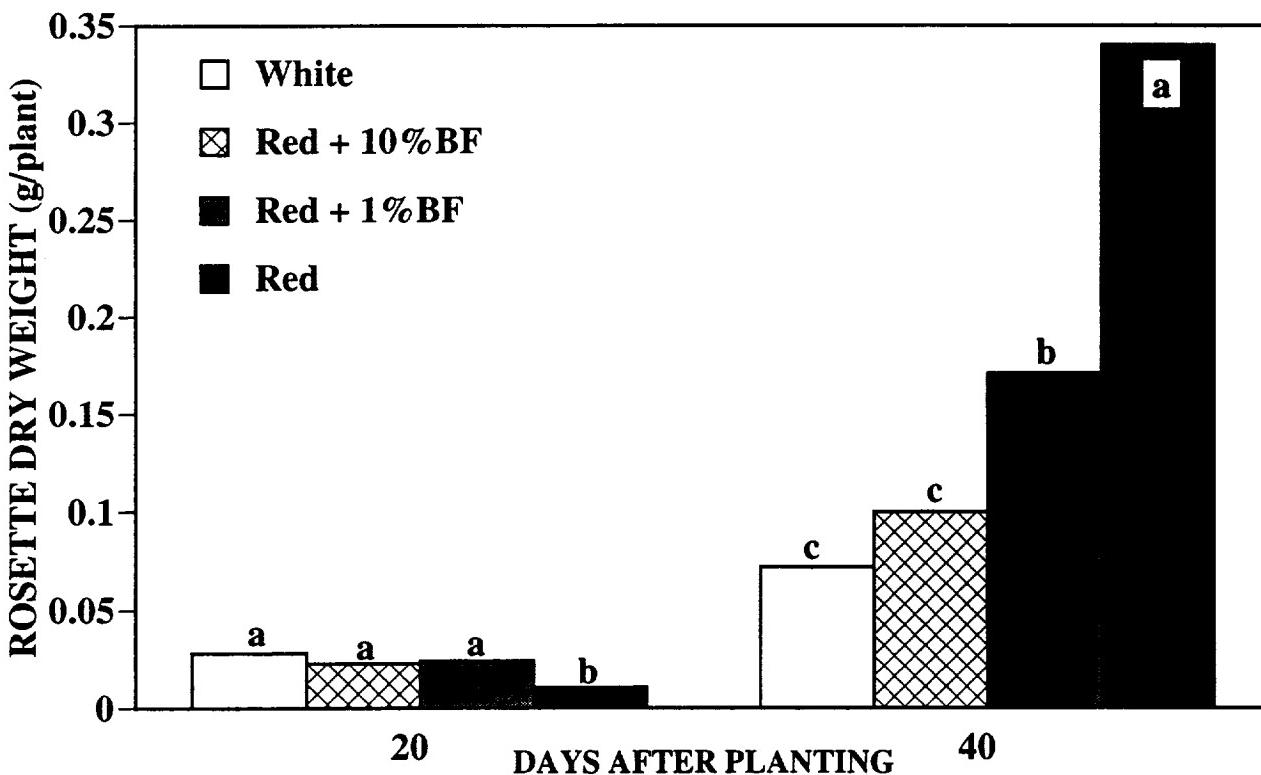


Fig. 16. Rosette dry weight of *Arabidopsis* plants grown for 20 or 40 days grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 20 or 40 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$).

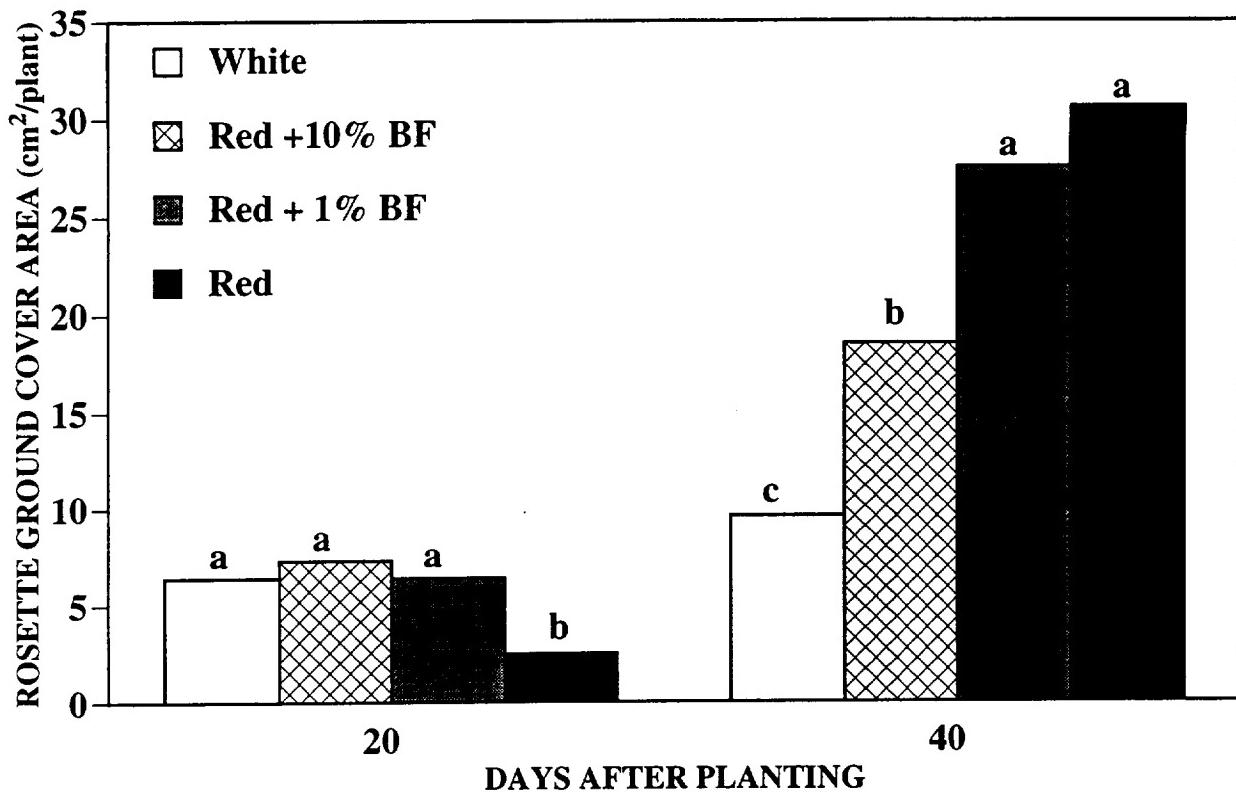


Fig. 17. Total rosette ground cover area of *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 20 or 40 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$).

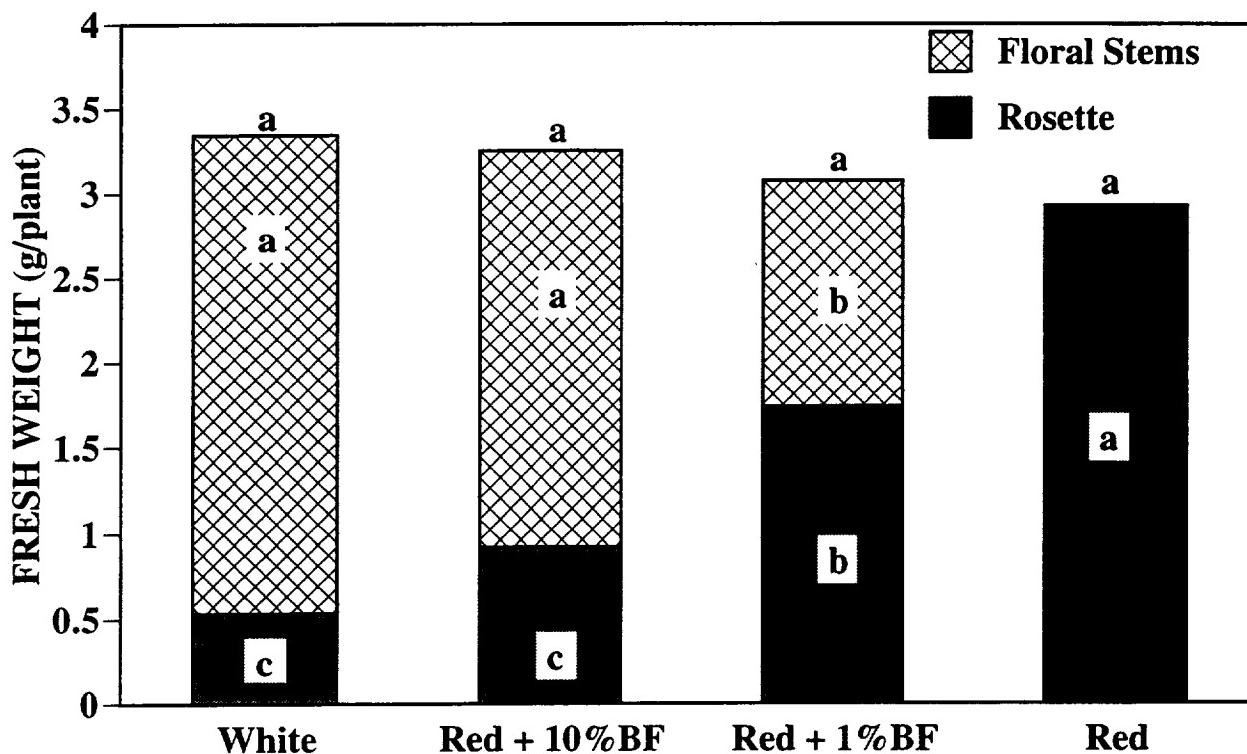


Fig. 18. Fresh weight of rosettes and floral stalks of *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 40 days. Similarly shaded portions containing different letters are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). The letters above the bars indicate significance for the combined plant dry weight.

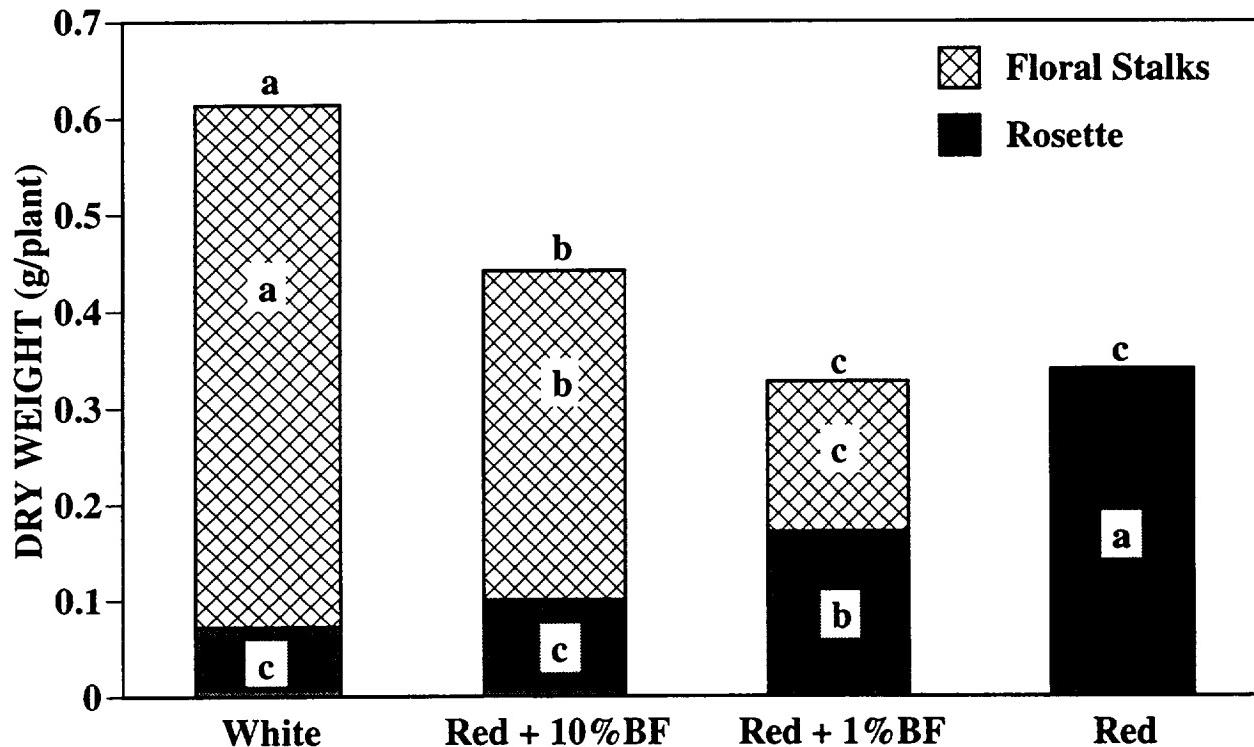


Fig. 19. Dry weight of rosettes and floral stalks of *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 40 days. Similarly shaded portions containing different letters are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). The letters above the bars indicate significance for the combined plant dry weight.

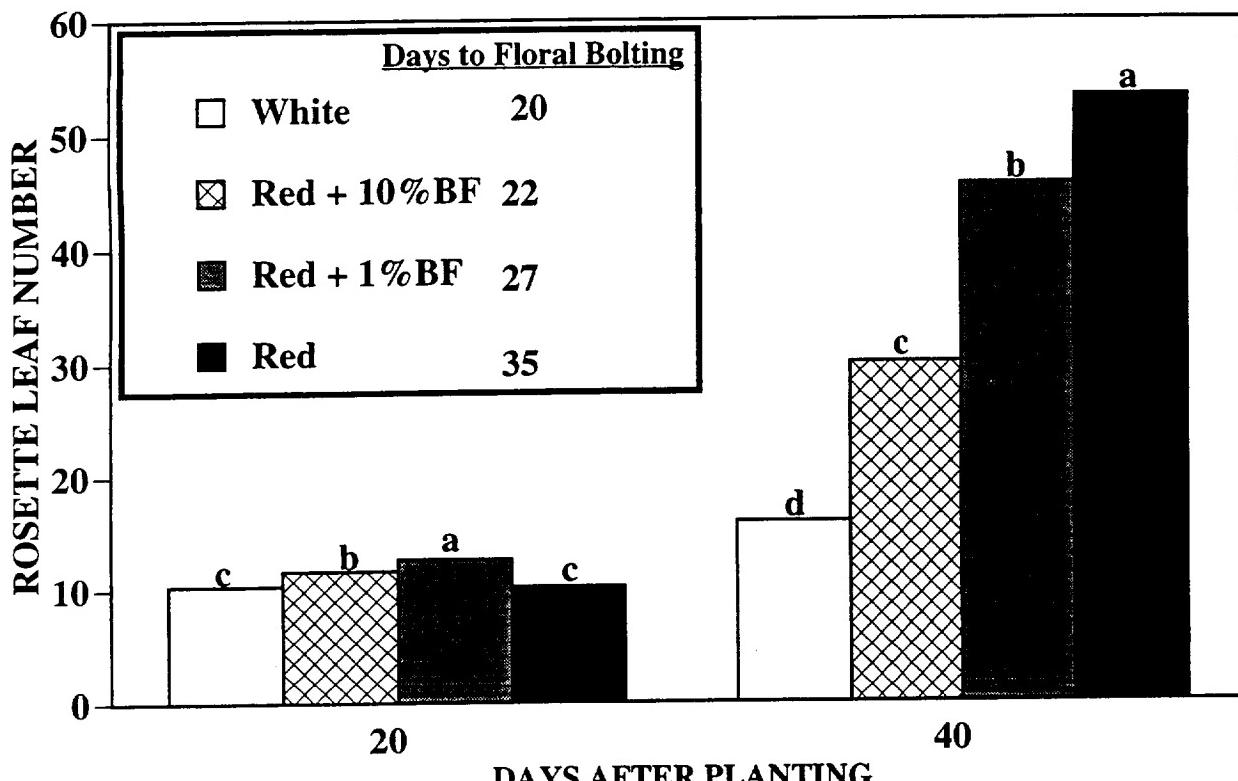


Fig. 20. Rosette leaf number (graph) and number of days to floral bolting (inset) of *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 20 or 40 days. Bars with different letters within each DAP are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$).

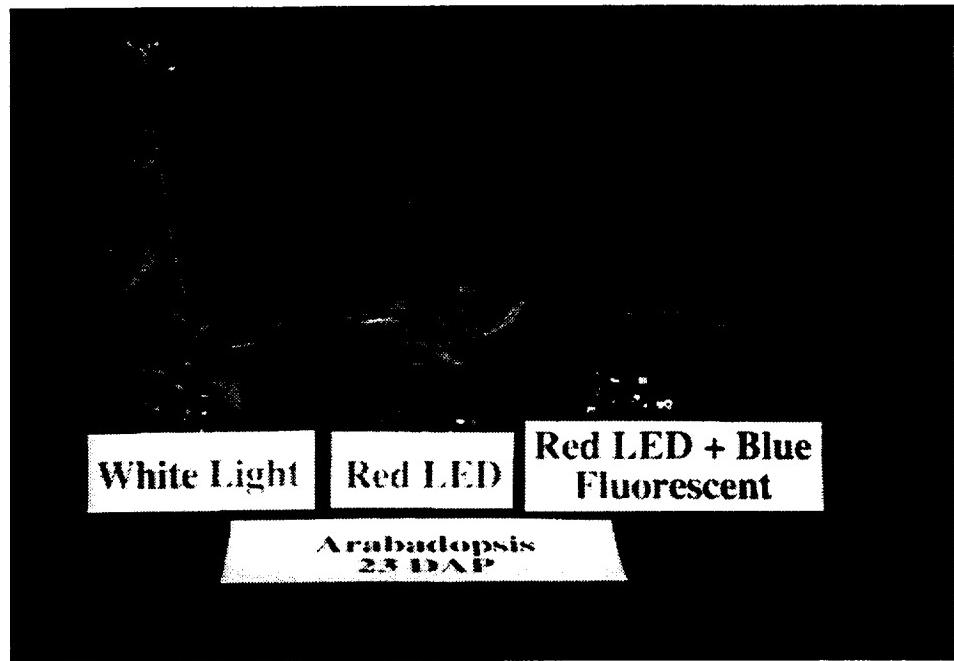


Fig. 21. *Arabidopsis* plants from white light, red LEDs only, and red LEDs + 1% BF light at 23 DAP. Note the unusual spiral leaf growth pattern in the plant (middle) grown under red LEDs alone.

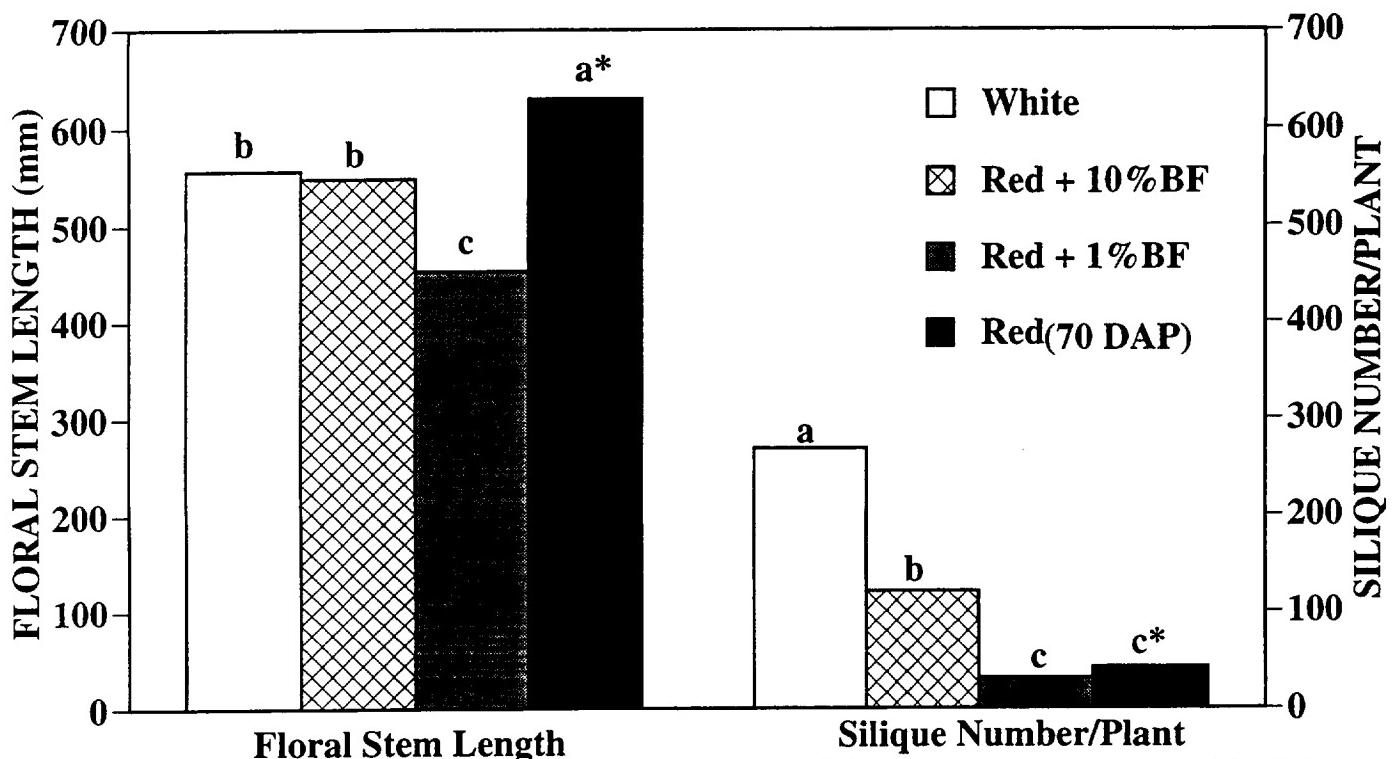


Fig. 22. Floral stem length and siliques number per plant of *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 40 days (except under red LEDs only where plants required approximately 60-70 days to set seed). Bars with different letters within each type of measurement are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). *Denotes mean at 70 DAP as opposed to 40 DAP.

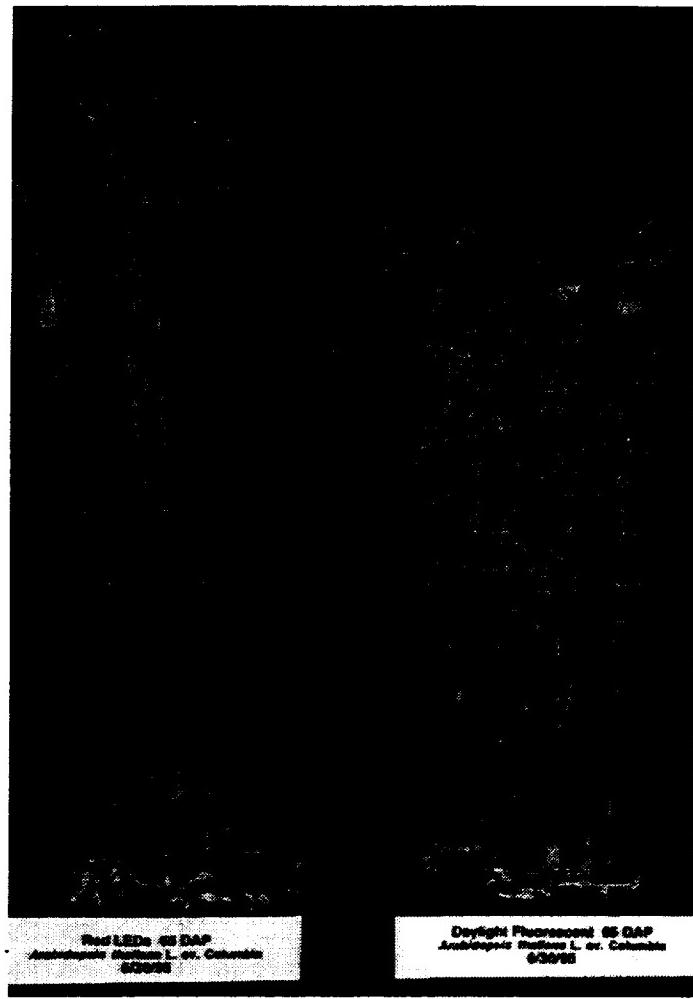


Fig. 23. *Arabidopsis* plants (7 plants/ARATRAY) from red LEDs (left) and white light (right) at 65 DAP. Note the large amount of vegetative growth and few mature siliques on the *Arabidopsis* plant grown under red LEDs as compared to the daylight fluorescent-grown *Arabidopsis*.

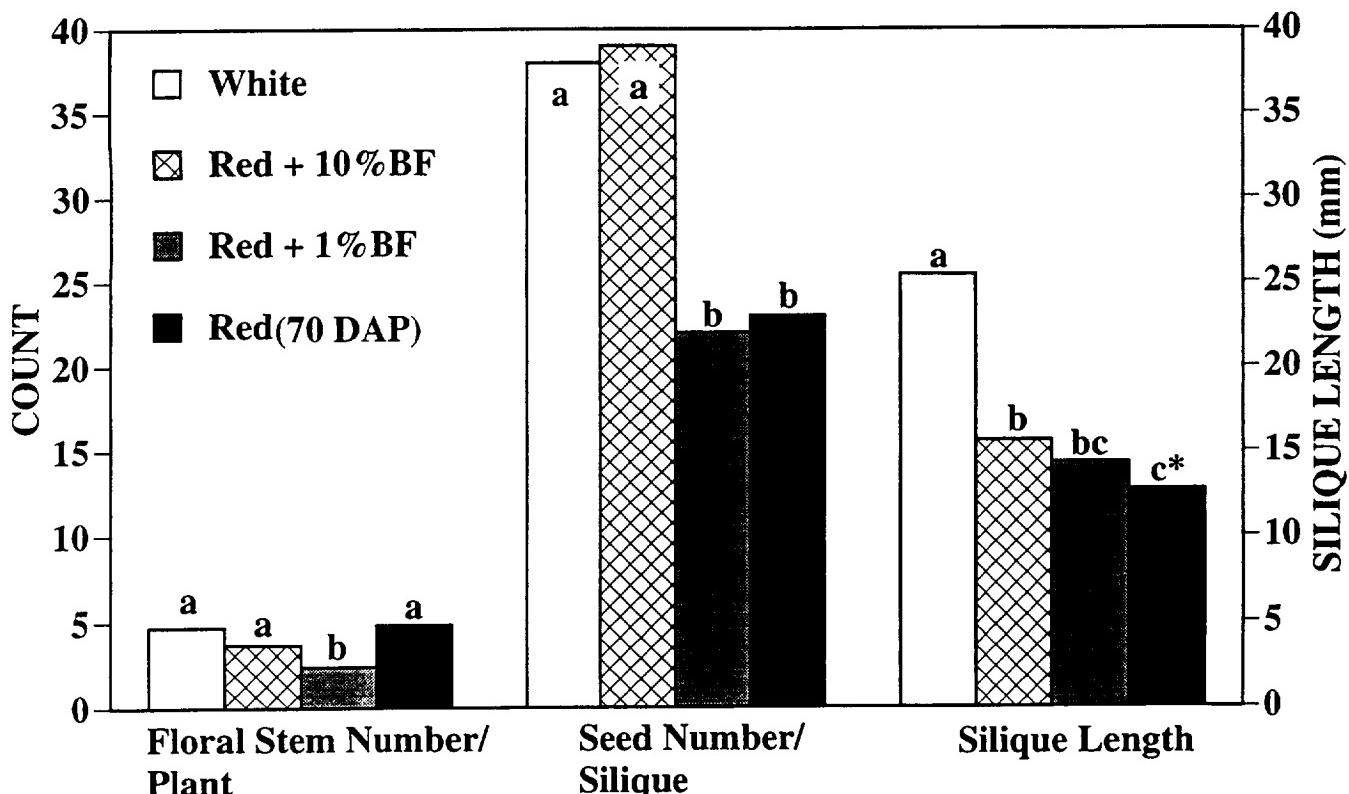


Fig. 24. Floral stem number, seed number per siliques, and siliques length of *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 40 days (except under red LEDs only which required 60-70 days to set seed). Bars with different letters within each type of measurement are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). *Denotes mean at 70 DAP as opposed to 40 DAP.

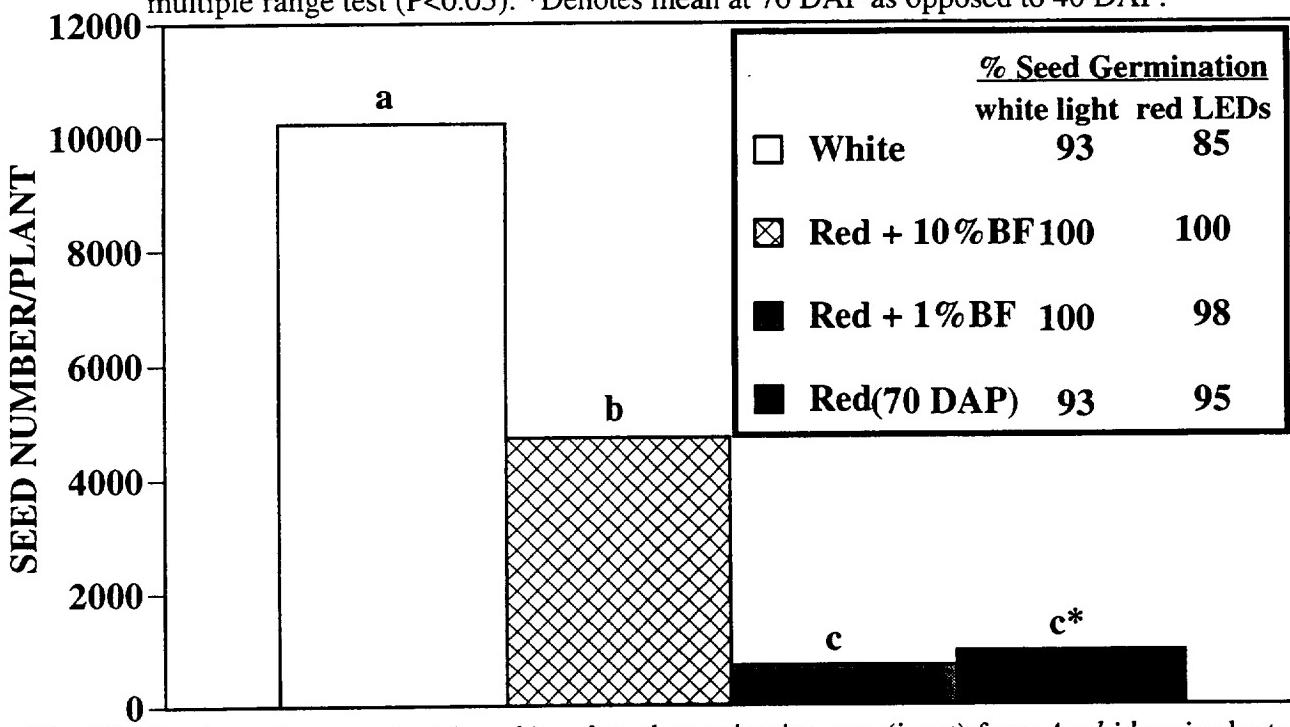


Fig. 25. Seed number per plant (graph) and seed germination rate (inset) from *Arabidopsis* plants grown under white light, red LEDs only, red LEDs +1% BF light, or red LEDs + 10% BF light for 40 Days (except the red LED treatment which required 60-70 days to set seed). Bars with different letters are significantly different based on ANOVA and Duncan's multiple range test ($P<0.05$). *Denotes mean at 70 DAP as opposed to 40 DAP.

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13. ABSTRACT (Maximum 200 words) To determine the influence of narrow-spectrum red light-emitting diodes (LEDs) on plant growth and seed production, wheat (<i>Triticum aestivum</i> L. cv Superdwarf) and Arabidopsis (<i>Arabidopsis thaliana</i> (L.) Heynh, race Columbia) plants were grown under red LEDs (peak emission 660nm) and compared to plants grown under daylight fluorescent (white) light and red LEDs supplemented with either 1% or 10% blue fluorescent (BF) light. Wheat growth under red LEDs alone appeared normal, whereas Arabidopsis under red LEDs alone developed curled leaf margins and a spiraling growth pattern. Both wheat and Arabidopsis under red LEDs alone or red LEDs + 1% BF light had significantly lower seed yield than plants grown under white light. However, the addition of 10% BF light to red LEDs partially alleviated the adverse effect of red LEDs on yield. Irrespective of the light treatment, viable seeds were produced by wheat (75-92% germination rate) and Arabidopsis (85-100% germination rate). These results indicate that wheat, and to a lesser extent Arabidopsis, can be successfully grown under red LEDs alone, but supplemental blue light is required with red LEDs to sufficiently match the growth characteristics and seed yield associated with plants grown under white light.			
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